

HAWAIIAN BIOGEOGRAPHY

EVOLUTION
ON A
HOT SPOT
ARCHIPELAGO

EDITED BY
WARREN L. WAGNER
AND V. A. FUNK

HAWAIIAN
BIOGEOGRAPHY

Smithsonian Series in Comparative Evolutionary Biology

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EVOLUTION ON A HOT SPOT ARCHIPELAGO

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WARREN L. WAGNER
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Preface

Isolated oceanic islands have long lured the evolutionary biologist. More than a century ago, Alfred Russell Wallace and Charles Darwin stressed how much could be learned about evolution by studying plants and animals on volcanic high islands. Of all the oceanic islands, the Hawaiian archipelago is often considered an unparalleled example of insular evolution. Several factors contribute to making this so. The Hawaiian chain is the most massive oceanic archipelago and has extensive ecological variation—from dry and mesic coastal environments to a wide array of inland habitats ranging from arid to the wettest on earth and ranging in elevation from sea level to 4,200 m. Moreover, the archipelago represents the longest, apparently regular, continuous formation of islands in a linear chronology in the world because of an incessant hot spot under the earth's mantle. Former high islands in the Hawaiian-Emperor Chain, once in a geographic position similar to today's eight high islands of the Hawaiian chain, were first formed during the Tertiary Period, at least 70 million years ago.

Perhaps the most important aspect of the Hawaiian Islands for evolutionary studies is their striking isolation. At more than 3,500 km from the nearest continental land mass, this most secluded archipelago has been colonized exclusively by waif elements. Also, repeated colonization by the same species is less likely. Stochastic colonizations were not confined to the first arrivals to the archipelago. As each new island was formed to the southeast of the existing islands, new opportunities for colonization were constantly presented. However, successful establishment on a new island may be more dependent on ability to colonize ecologically younger sites or a wider range of habitats not available on older source islands.

All these features combine to give the Hawaiian archipelago an extraordinary terrestrial biota that includes approximately 700 fungi, 800 lichens, 260 mosses, 180 pteridophytes, 1,000 angiosperms, 1,000 land snails, 230 terrestrial arthropods (excluding insects), 5,000 insects,

112 birds, 5 fresh-water fishes, and 2 mammals. Endemism in this biological array ranges from about 50% for mosses and 89% for angiosperms to 99% for insects. Many of the terrestrial groups of Hawaiian organisms are represented here, including insects (Chapters 4 to 7), spiders (Chapter 8), birds (Chapter 9), and flowering plants (Chapters 10 to 16). There are, however, omissions including lichens, pteridophytes, bryophytes, and terrestrial snails, some of which have not radiated and others that have no appropriate data.

Hawaiian geology continues to develop at a rapid pace, and unfortunately geology texts usually do not emphasize the fundamental geologic features pertinent to the biologist, especially the biogeographer. We are fortunate to be able to include a chapter that provides an up-to-date summary of the features relevant to island biogeography.

This volume, which grew out of a symposium cosponsored by the American Society of Plant Taxonomists and the Association of Tropical Biology in 1992, was catalyzed by the auspicious coincidence of three developments. First, during the three decades since the original articulation of the hot spot theory of mid-Pacific archipelago formation, tremendous advances have been made in our understanding of the geologic processes involved in the formation and history of this conveyor-like archipelago. Second, convenient phylogenetic methods are now widely available and used by most researchers. Finally, the past decade has witnessed a considerable increase in the number of researchers investigating a wide array of the evolutionary radiations of Hawaiian terrestrial organisms.

The chapters of this collaborative work represent the first attempt to test the idea that independently derived groups of Hawaiian organisms exhibit similar patterns of colonization and differentiation that relate directly to the unique geologic history of this oceanic archipelago. Each participant applied phylogenetic methods to morphological or molecular data to generate phylogenetic hypotheses, secondarily deriving biogeographic hypotheses. Rather than mere summaries of the participant's research, these studies mostly present new data and analyses. Each contributor has used a consistent methodology to allow evolutionary patterns of different groups to be directly compared in our search for common and discordant patterns. Patterns generated in these studies have been further manipulated to test ideas about evolution, such as innovation in breeding systems, behaviors, or ecology in an insular environment.

This volume represents the first detailed biogeographic study of Hawaiian organisms other than isolated exceptions such as the Hawaiian

Drosophila and S. Carlquist's innovative work culminating in his 1974 book *Island Biology*. This collaboration has brought together a majority of the contemporary biological researchers on the terrestrial Hawaiian biota who have appropriate and sufficient data. Indeed, this may represent the first attempt to analyze a significant proportion of the plants and animals of any natural area using a formal, rigorous approach, such that the results can be compared across different taxonomic groups. By collecting and synthesizing data for the Hawaiian biota, we not only add new understanding of the biogeography of the archipelago but may further kindle new ideas toward an understanding of evolution on islands.

Acknowledgments

The idea for this volume grew out of the compatible interests of the coeditors. One of us (W.L.W.) has a deep interest in Hawaiian biogeography, generated through years of collaboration with Derral Herbst and many others on the classification of Hawaiian flowering plants. The other (V.A.F.) has long been concerned with the use of phylogenetic patterns to study biogeography and speciation. Discussions between the coeditors in 1990 concerning application of phylogenetic systematics to the study of island species radiations resulted in a paper presented at the 1991 Society for the Study of Evolution meetings in Hilo (developed into Chapter 10). We are grateful to many colleagues, especially Sherwin Carlquist, Hamp Carson, Neal Evenhuis, Chris Haufler, Derral Herbst, Scott Miller, Lynne Parenti, Ann Sakai, and Steve Weller for insights, advice, and encouragement during this project. We thank all the contributors for their enthusiastic participation in the 1992 American Institute for Biological Sciences (AIBS) symposium in Honolulu and their willingness to contribute, often unpublished new data, to this volume.

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Each chapter in this volume was peer-reviewed by at least two reviewers, one from among the volume contributors and the other an outside review. Each chapter was also reviewed by both editors and the technical editor. Because this project brought together so much of the biological expertise on the Hawaiian Islands, we depended on a considerable number of the contributors as reviewers of other contributors' chapters. We thank them all. In addition to these reviews, each chapter received one or more reviews from a specialist outside of the project

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We especially thank Lucy Julian and Jim Nix for their support, encouragement, and patience during the preparation of this book.

The Hawaiian Islands, unique among geographic regions on earth, are a fascinating place to study evolutionary biology. We hope that the studies here not only spur new insights for science but that the new understanding of the nature of the endemic organisms in the Hawaiian Islands will help promote their conservation. In that light, any royalties from the sale of this book will be contributed to the National Tropical Botanical Garden research program, which is contributing much to exploration, study, and conservation of the plants of the Hawaiian and other Pacific islands and therefore also the fauna that depend on them. This comes at an especially critical time as they recover from the devastation of Hurricane 'Iniki.

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1

Introduction

SHERWIN CARLQUIST

The chapters in this book represent a quantum advance in our knowledge of Hawaiian organisms. Although advances have been made in this field in each decade since the European and American voyages that first brought specimens to interested scientists, advances in the past two decades have been quite phenomenal. Acceleration of our knowledge of Hawaiian organisms represents a number of coincident advances, mostly of a technological nature.

Ease of travel to the Hawaiian Islands is responsible for bringing a greater number of scientists to the islands. The Hawaiian chain is now so readily accessible for field work that many workers have taken the opportunity to study its organisms, the most remarkable oceanic island biota in the world. Ease of accessibility coincides with a time when native Hawaiian species are, to a large extent, still extant. Most of the key genera and species necessary for development of a clear picture of the evolution of most groups in the Hawaiian biota are still in existence. But one should not be complacent: Although many species remain to be studied in many respects, some have gone extinct and a number are endangered, with doubtful prospects for persistence of many of these species into the next century. This book, then, should be treated as an accomplishment but also regarded as an urging for still more work on the Hawaiian chain as well as on other oceanic islands that face similar threats to native biota.

Another advance represented by this volume is the application of a uniform analytic technique, cladistics. Cladistic results have been ex-

pressed both in taxonomic and in geographic terms: the latter as the sequence of colonization of islands and even areas within islands. The application of cladistics to all groups analyzed has permitted the comparison of patterns, so that the range of phyletic and geographic patterns in evolution of the groups can be analyzed. A comparison of cladistic results, particularly the area cladograms, is offered in the terminal chapter by Funk and Wagner. My purpose in this chapter is to cite noteworthy results other than those Funk and Wagner analyze and to call attention to their probable significance. In many instances, attention is called to unsolved questions of special interest. There should be no doubt in any reader's mind that despite the dramatic results of this volume, many fascinating studies remain to be done—and many of these can be performed quite simply and easily.

HISTORICAL PERSPECTIVE

Our current knowledge of Hawaiian organisms has developed from traditional systematic studies and from newer approaches and technologies. Before considering those advances, we must pay special tribute to those earlier systematists who not only prepared systematic monographs of value but also were careful observers of the biology of Hawaiian organisms. Notable among these are Perkins (1913) and Zimmerman (1948). It should be stressed that for almost any Hawaiian animal species, we still would like to know more about habitat preference, diet, and behavioral details. For almost any Hawaiian plant species, we would welcome more information on ecological preferences, reproductive biology, and dispersal biology.

In plants, workers notable for contributing data on chromosome number and morphology include George W. Gillett and Carl Skottsberg and, more recently, Gerald D. Carr and D. W. Kyhos (1981, 1986). I attempted anatomical studies of the Hawaiian tarweeds (Carlquist, 1957b, 1959a,b) and other groups. In animals, work on Hawaiian species of *Drosophila* was a key to using techniques beyond morphology. Hawaiian species of *Drosophila* resisted the ordinary *Drosophila* laboratory cultural techniques because of their specialized food requirements. However, when cultural media based on extracts of Hawaiian plants were developed, the study of polytene chromosomes was enabled (see Chapter 5). Using chromosome data, the phyletic and therefore geographic interrelationships of *Drosophila* species and species groups could be

elucidated (the names of the workers involved in the massive effort devoted to Hawaiian Drosophilidae can be found in Chapters 5 and 6).

Polytene chromosomes are not, however, available for Hawaiian organisms other than Drosophilidae, so other tools for determination of genetic interrelationships must be sought; ultimately, the most satisfying information is currently derived from molecular studies directly using DNA. One notable example of this approach is the work of Tarr and Fleischer (Chapter 9), which suggests revision in the traditionally recognized subfamilies and genera of Hawaiian honeycreepers.

LOCATION AND TIMING OF ORIGINS OF HAWAIIAN AND OTHER ISLAND FLORAS AND FAUNAS

The recency of adaptive radiation and other types of speciation is evident in such genera as *Drosophila* (Chapters 5 and 6), *Geranium* (Chapter 10), *Tetramolopium* (Chapter 11), and *Clermontia* (Chapter 15), as well as in some species groups in other examples, such as the Hawaiian tarweeds (Chapter 13). We can certify the recency of this evolution because of the high degree of certainty of the area cladograms and the excellence of potassium-argon datings available for islands in the Hawaiian chain (see Chapter 2). No scientist reading the massive evidence this book presents for speciation—with many events of adaptive shifts, as evident in the tarweeds (Chapter 13) and *Schiedea* (Chapter 12)—could doubt that there has been, in genus after genus, autochthonous evolution, especially that involving adaptive radiation.

Europeans studying Atlantic islands have views of evolution on islands that contrast starkly to the amazing patterns demonstrated in this book. For example, Berry (1992), in a section of his paper entitled “Modern Island Biology,” stated that “post-colonization adaptation probably plays little part in the origin of most endemism; although natural selection affects island biotas just as much as—perhaps more than—continental ones, the main differentiation of island forms is usually the result of the chance characteristics of the original colonists of each species.” Likewise, Cronk (1992) generalized for islands of the world, “If the relict nature of oceanic island endemics is accepted, then these plants become a key to understanding biogeographical and taxonomic patterns. They indicate groups in which extinction has occurred, and the degree of taxonomic and geographical disjunction may reveal something of the extent of that extinction.”

European workers apply the relict hypothesis of oceanic island endemics to manifestations that are demonstrated in this volume to result from adaptive radiation. For example, the cladograms for *Tetramolopium* (Chapter 11), the Hawaiian tarweeds (Chapter 13), and the Hawaiian lobelioids (Chapter 14) show evolution of increased woodiness on the Hawaiian Islands. However, for the Atlantic islands, Sunding (1979) interpreted similar patterns in exactly the reverse fashion: "That a large proportion of the Macaronesian vascular flora is of a great age is shown not only by its present-day distribution patterns with often large distribution gaps to the nearest related taxa, but also by features like the prevailing woody life-form in genera elsewhere represented by herbs (*Echium*, *Sonchus*, *Limonium*, *Plantago*, *Sanguisorba*, etc.). . . ."

Cronk (1992) regarded the St. Helena Island endemic monotypic genus *Petrobium* as being "Miocene . . . probably older than 10 My," although the origins of the entire family Asteraceae are likely only a little before Miocene—upper Oligocene—and *Petrobium* is by no means primitive in the family (Jansen et al., 1991). Cronk (1992) apparently was impressed by resemblances of *Petrobium* to the Polynesian genus *Oparanthus* and regards this two-ocean distribution as indicative of great age. In fact, both *Petrobium* and *Oparanthus* are recent derivatives of *Bidens*—so recent, in fact, that Stuessy (1988) justifiably reduced both *Oparanthus* and *Petrobium* to *Bidens*.

Those European workers who do believe in the relictual hypothesis cited above do not mention potassium-argon dates for islands. Moreover, molecular data, one of the great strengths of this book, have been applied to only a few situations on Atlantic islands. Very likely, the picture of evolution on Atlantic volcanic islands will change to resemble more closely the findings from the Hawaiian chain when evidence from geology and DNA analysis is available and when cladistic methods are used.

One of the fascinating implications of this volume concerns the role of now-vanished islands of the Hawaiian chain in contributing to the flora and fauna we now see on the present high islands. We are now familiar with the sequence beginning as early as 70 to 80 million years ago (Ma) at Suiko Seamount, proceeding through the bend in the chain at Daikakuji Seamount at about 43 Ma, terminating at Kilauea and Lo'ihi, the seamount that has not yet surfaced but is still actively growing. There is a continuous chain, but has there been biological continuity? In other words, are there any plants or animals currently on the high islands whose ancestors were once on the earliest islands, such as Suiko? There are plants in the current Hawaiian flora one might be tempted to think

ancient in origin because of the families to which they belong, such as *Eurya* (Theaceae) and *Cryptocarya* (Lauraceae), but we have only one Hawaiian species each of these, and determining the date of their separation from the remainder of their respective genera may be impossible. However, both *Eurya* and several genera of Lauraceae are native to both the Ogasawara (Bonin) and Volcano Islands, volcanic islands that are indubitably recent, have never had any contact with the Japanese mainland, and are far enough from Japan so that one must invoke long-distance dispersal as the mechanism for populating these islands (Kobayashi and Ono, 1987).

If origins of the Hawaiian flora and fauna were on islands formed previous to Kaua'i and Ni'ihau, we would expect to see, in an appreciable number of instances, two or more quite distinct lines present on Kaua'i and post-Kaua'i islands, lines that on Kaua'i already show long divergence. This would be evident in cladograms and in the nature of the molecular data that might be used in cladograms. This kind of pattern is seen in several of the cladograms presented in this volume. Other cladograms suggest origin on Kaua'i or an even younger island—even on the island of Maui in the case of *Tetramolopium*. Another example is *Clermontia*, where the origin of at least the present extant species can be traced to the youngest island, Hawai'i; however, the origin of the ancestors of *Clermontia* may have been on an older island (see Chapter 14). These patterns show that speciation and evolution on oceanic islands are quite recent, and we need not hypothesize radiation on continents followed by dispersal of the products of that radiation to islands, as Berry (1992) or Cronk (1992) did.

There are no spectacular relicts on the present Hawaiian chain, and calling any of them ancient is a misnomer if one compares Hawaiian plant or animal groups with those on continental islands. Even though the Emperor Seamounts could have theoretically served as stepping-stones for plants and animals to migrate to the present-day high islands, we lack evidence that they did so. Although some of the chapters in this volume mention possible origins of groups as far back in the chain as French Frigate Shoals, Necker, or Nihoa (when they were high islands), none of the Leeward Islands earlier than those have yet been placed into consideration, and indeed, the geologic evidence shows the chain was dormant before Kure long enough so that no colonization from pre-Kure islands (which would have eroded to atolls or seamounts before Kure or later islands arose from the sea) can be hypothesized (see Chapter 2). A few pre-Kaua'i but post-Kure floristic or faunistic elements might have

been displaced by and thereby extinguished by more recent colonists. Such genera as *Alectryon*, *Hesperomannia*, *Hibiscadelphus*, and *Kokia* suggest older immigrants that are no longer common and were already disappearing in prehuman times.

NEW EVIDENCE, NEW IDEAS

The geologic overview by Carson and Clague in Chapter 2 performs an enormous service by refining our ideas on age and size of islands in the Hawaiian chain. These are of great importance in providing a chronology for evolutionary events specified in the various cladograms. In this connection, the point is made by Carson and Clague that each of the post-Wai'anae volcanoes was at some earlier time coalescent with the volcano preceding it in the series. The disappearance of huge portions of islands, or even the entire above-water portions of an island, by catastrophic slumps will be a concept new to most readers. The most important contribution of Chapter 2, where biogeography is concerned, is the summary of evidence that the Hawaiian chain was dormant for long enough before the emergence of Kure so that no colonization from pre-Kure islands can be hypothesized. They had eroded to atolls or seamounts before Kure emerged, so that no high-island elements from older islands were available to Kure or the islands that emerged later than Kure. This should certify the role of long-distance dispersal in colonization of the Hawaiian chain, and the consequent importance of the Hawaiian chain in discussions of long-distance dispersal has been magnified accordingly.

Chapter 4 by Shaw deals with evolution of Hawaiian crickets. Noteworthy is the fact that all cricket species are one-island endemics, demonstrated by DNA evidence but not always clear from morphology. Rapidity in species formation is clearly suggested. Shaw also demonstrates that "the Hawaiian tree crickets, as well as the swordtail crickets, have diverged from their original founder lineages to such a degree that they were taxonomically misplaced by Perkins (1899) and Zimmerman (1948)."

Chapter 5 on Hawaiian *Drosophila* by Kaneshiro, Gillespie, and Carson is notable for providing a thorough review of this fascinating topic. It updates the estimate of Hawaiian *Drosophila* species to a startling 1,000, of which a little more than half (511) have been described at present. This emphasizes the fact that the exploratory phase in Hawai-

ian biology is not yet complete in some groups where alpha taxonomy is concerned and clearly not complete for any Hawaiian plant or animal group where understanding of species biology is concerned. Readers will be fascinated by the close relationship in chromosomal sequences between the Hawaiian *D. primaeva* and *D. colorata* of Japan.

When molecular approaches are used for study of Hawaiian Drosophilidae (see Chapter 6 by DeSalle), no single continental species or species group clearly appears as ancestral to the drosophilids. There are hints from molecular data that Hawaiian drosophilids might date back 20 to 40 Ma, although one would like more molecular clock indicators. At the other extreme, many readers will be surprised by the way molecular data can elucidate the “microbiogeographic” sequences in colonization of the newest areas on the island of Hawai‘i.

Asquith (Chapter 7) shows that taxonomic identity of host plants is of great significance in analyzing phyletic patterns of *Sarona* (Heteroptera). Shifts in host plant preference can be placed on cladograms. Because Asquith claims these shifts in host plants may mediate sympatric events of speciation, the significance of his analysis may go well beyond *Sarona* and may be applicable to other claimed instances of sympatric speciation. Asquith hypothesizes origin of *Sarona* on a pre-Kaua‘i island.

Gillespie and Croom (Chapter 8) offer the only contribution on spiders, whose evolution on islands has not been subject to much discussion. The Hawaiian species of *Tetragnatha* are diverse with respect to colors, shapes, sizes, ecological preferences, and behaviors, in contrast to the relative uniformity of the genus elsewhere in the world. The Hawaiian species appear to have originated on Kaua‘i; speciation has been allopatric, as in most Hawaiian plant and animal groups, with sister species in the non-web-building group never occupying the same volcano or even the same island.

Tarr and Fleischer (Chapter 9) uncover some unexpected interrelationships in their analysis of Hawaiian honeycreepers. For example, the Kaua‘i Creeper (*Oreomystis bairdii*) is apparently the sister species of the thick-billed Laysan Finch (*Telespiza cantans*). Two of the honeycreepers—*Melamprosops* and *Paroreomyza*—may not be honeycreepers at all but rather products of an independent colonization. However, the honeycreeper analysis makes one wonder how topology of the cladogram would change if DNA were available for very rare or extinct species. Acknowledging that their study is not definitive, Tarr and Fleischer offer a molecular clock figure of 3.5 Ma for the origin of the Hawaiian honeycreepers. This date is of considerable interest because the Hawaiian

honeycreepers appear to be one of the older elements in the Hawaiian fauna.

Funk and Wagner (Chapter 10) analyze seven flowering plant phylads with morphology-based cladograms. The results underline the familiar old island to young island progression seen in the majority of Hawaiian groups analyzed. However, the Hawaiian species of *Geranium* may well have originated on Maui and spread to both Kaua'i and Hawai'i. Their analysis of *Hesperomannia* shows that the basal Kaua'i species, *H. lydgatei*, is rich in autapomorphic characters. The likelihood that the asteraceous genus *Remya* represents an extension of the Pacific genus *Olearia*, as hypothesized by Wagner and Herbst (1987), is underlined by the Funk and Wagner cladogram and resolves relationships of this genus, earlier considered of uncertain affinities.

Lowrey (Chapter 11) analyzes the evolution of another genus of Asteraceae, *Tetramolopium*, with respect to geography, habitat, and ecological change. The results should be read by Europeans who have a relict view of oceanic island floras and faunas. Lowrey shows that *Tetramolopium* has traveled from New Guinea to Maui, with subsequent radiation to other main islands (except Kaua'i, on which *Tetramolopium* is absent). Especially interesting is the occurrence of *T. sylvae* both on Maui and on Mitiaro in the Cook Islands. This is the result of a relatively recent event of long-distance dispersal from Maui or Moloka'i to Mitiaro, and diversification on the latter island is already in progress. Lowrey's results demonstrate clearly the occurrence of long-distance dispersal, the rapidity of adaptive radiation, the marked nature of ecological shift, and the change from less to more woody autochthonously in volcanic oceanic islands.

Wagner, Weller, and Sakai (Chapter 12) study the complex formed by two endemic genera of Caryophyllaceae, *Alsinidendron* and *Schiedea*. They show that persistent field work can uncover both new and supposedly extinct species. The inclusion of these in the latest cladograms of the complex has resulted in greater resolution. *Schiedea* has shown several shifts between wet and dry habitats, so that the original habitat for the complex is uncertain. Likewise, there have been shifts from subdioecy to gynodioecy, as well as to hermaphroditism. Such changes should be kept in mind by those who tend to have a unidirectional view of these trends. Analysis of the *Alsinidendron-Schiedea* complex suggests a pre-Kaua'i origin for the group, although not markedly earlier than the emergence of Kaua'i.

The radiation of the Hawaiian tarweeds or silversword alliance (see Chapter 13 by Baldwin and Robichaux) is surely the most spectacular example of adaptive radiation on islands in the world. That fact alone makes any detail about this complex of great interest in contributing to this amazing story. The ancestry of the Hawaiian tarweeds is in the Californian Floristic Province and very likely from subshrubby montane tarweeds of northern California such as *Raillardiopsis* or *Madia* species. The cladograms for the complex offer an interesting paradox: Although *Argyroxiphium* is the oldest of the genera to have originated from the single ancestral colonization, it does not occur on Kaua'i or O'ahu. The authors entertain the possibility of a pre-Kaua'i origin for *Argyroxiphium*. If pre-Kaua'i, the origin was certainly not much earlier, because the genetic distance between *Argyroxiphium* and the other genera, for which origin on Kaua'i is indicated, is not very great. Montane Californian tarweeds likely to have been close to types ancestral to the Hawaiian complex exist in a climate at 1,000 to 1,500 m much like the climates at 2,200 to 2,800 m in the Hawaiian Islands. This latter elevational range has been gone from Kaua'i for perhaps the past 1 to 2 million years and also has been absent from O'ahu for that long as well. Transfer of *Argyroxiphium* from a now-vanished dry alpine zone on Kaua'i to Maui (where it has radiated into wet habitats from dry alpine sites) seems entirely possible. If we imagine an *Argyroxiphium* origin on a pre-Kaua'i island, we have to imagine it inhabiting Kaua'i or both Kaua'i and O'ahu, yet not radiating into any of the habitats now present on these islands and not surviving in those habitats. Had *Argyroxiphium* originated on a pre-Kaua'i island, it is likely to have left some species on Kaua'i and/or O'ahu because of the capability of the genus for radiating rapidly into a range of habitats. A rapid diversification of a tarweed from montane California in a high-montane habitat on Kaua'i into *Argyroxiphium*, *Dubautia*, and *Wilkesia* seems entirely conceivable on the basis of presently available data. In fact, the two islands before the Ni'ihau-Kaua'i complex would not have been suitable as sites of colonization for an alpine tarweed: The maximum height of Nihoa was 1,300 m and that of Necker 1,100 m (see Chapter 2), so those two islands would have lacked alpine regions in which *Argyroxiphium* could have originated if its origins were alpine. Certainly, most of the evolution of the complex has taken place rapidly on Kaua'i, according to the available data. This scenario indicates how much we know about the evolution and origin of this and other Hawaiian groups, even if a few pieces of information are elusive.

The Hawaiian lobelioids are hardly less spectacular than the tarweeds in their adaptive radiation. Information about the lobelioids is contributed by Givnish et al. (on *Cyanea*, Chapter 14) and by Lammers (on *Clermontia*, Chapter 15). The chapter on *Cyanea* also contains an account of the radiation that led to *Brighamia*, *Delissea*, *Cyanea*, *Rollandia*, and *Clermontia*. The fact that most of the traditional genera can still be maintained despite their closeness is interesting. However, of considerable significance is the fact that *Brighamia* and *Delissea* are sister genera and had a lowland (and therefore moderately dry forest) origin. The affinities of *Brighamia* have hitherto been uncertain because of its highly distinctive features. Givnish et al. entertain the interesting speculation that the prickly (thorny) *Cyanea* species originated in response to pressure from now-extinct large browsing birds, the skeletons of which have recently been found. Givnish et al. present carefully assembled circumstantial arguments and draw on a parallel with the defenses of New Zealand plants, defenses now generally accepted as response to the herbivory of the moa or other large birds, as I hinted earlier (Carlquist, 1965). What Givnish et al. do not address is why the prickly *Cyanea* species in the Hawaiian flora have apparently increased in defensive capabilities, whereas despite rapid plant evolution, no other Hawaiian angiosperms have increased either physical or chemical defenses, so far as we know. On the contrary, defenses of Hawaiian angiosperms have plummeted to the lowest levels seen on any oceanic islands, suggesting that large herbivorous birds have had little or no effect.

In New Zealand, on the contrary, physical defenses are numerous (juvenile leaves of Araliaceae and other families, spiny leaves in *Aciphylla* and *Olearia*, and a large number of species of divaricating shrubs). Chemical defenses in the New Zealand flora are also much higher than in the Hawaiian Islands. The moas undoubtedly had a much longer tenure on New Zealand than did the large herbivorous birds on Hawai'i, but many of the New Zealand plant groups with defenses are the same or close to the plant groups on Hawai'i and are relatively recent (e.g., *Olearia*, *Remya*). That such likely recent immigrants to the native Hawaiian flora as *Argemone* and *Rubus* have lost most of their prickliness despite the presence of the large herbivorous birds is mystifying. My earlier suggestion that land mollusks (but definitely not Achatinellidae or Succinidae, which graze on surface algae and fungi) might have posed a threat to *Cyanea* was based on the tendency of mollusks to graze more on lower leaves of plants, neglecting upper leaves, which tend to be drier. Prickles in *Cyanea* and *Rollandia* tend to occur in wet habitats, which

tend to be densely vegetated and perhaps thus less accessible to large herbivorous birds than the more open habitats, which are lacking in prickly *Cyanea* species.

The fascinating results of Lammers in *Clermontia* suggest that this genus had its origin on the very new island of Hawai'i. Lammers's data seem to support this clearly, and it is entirely plausible to me. The rapidity of speciation and diversification of floral forms and sizes in *Clermontia* show how explosively plant evolution can occur on oceanic islands, countering the contentions of those who hold the relict hypothesis for oceanic island species. Migrations of a genus from a younger island to an older island require hypothesizing an open niche, and open niches are presumably fewer on older islands than on younger islands. *Clermontia clermontioides*, the sole species of the genus on Kaua'i, may have been able to colonize Kaua'i because its habit is epiphytic or semiepiphytic; the epiphytic habitat is, by definition, a pioneering habitat.

Patterson's analysis of *Scaevola* (Chapter 16) clarifies the origins of the Hawaiian species of this group, confirming that at least two introductions account for the presently native species on the Hawaiian chain. One would like to know how the topology of the cladogram would change if DNA data were available and if species such as the widespread *S. plumieri* and the many Australian species (especially those with fleshy fruits) were included. Inclusion of these would clarify the migration of the genus into the Pacific and the origin of the widespread beach *Scaevola*, *S. sericea*. I note with interest Patterson's observation, based on cladistic results, that dry country species of *Scaevola* have lost dispersibility to a lesser extent than have the wet forest species, which accords with my thesis that loss of dispersibility is much more abundant in Hawaiian plants of wet forests than those of dry forests (Carlquist, 1974).

NATURE OF SPECIATION ON THE HAWAIIAN CHAIN

One theme clear from these chapters is that evolutionary diversification on the Hawaiian Islands has been recent and has taken place autochthonously. Nevertheless, diversification has been profound, involving more than just a few morphological features. Robichaux et al. (1990) showed genuine physiological diversification among Hawaiian tarweeds: They are not doing similar things in different places; they are just as diverse in physiology as any selection of species from their various

habitats. The leaf anatomy of the Hawaiian tarweeds also shows exceptional diversification (Carlquist, 1957a, 1959a,b). Likewise, the Hawaiian honeycreepers differ not just in bill shape but in such features as tongue morphology as related to their diverse food sources (Amadon, 1950). These examples are cited because there is some tendency to believe that adaptive radiation on islands is less pervasive in diversification of its products than adaptive radiation on continents. There are some spectacular examples of speciation on the Hawaiian chain that do not involve adaptive shifts—for example, the agate shells (Achatinellidae)—but these would never be cited as examples of adaptive radiation but rather as examples of speciation that does not involve radiation into different habitats.

Despite the genuine morphological, ecological, physiological, and anatomical diversification of Hawaiian plants, there has apparently not been concomitant genetic change. For example, all the Hawaiian tarweeds can be crossed with each other, with little if any interspecific sterility evident (Carr and Kyhos, 1981, 1986). This contrasts with the Californian tarweeds, in which strong sterility barriers among species are common, and one can cite instances of strong sterility barriers even within species (Clausen, 1951). This tendency also appears to be true of other groups in the Hawaiian flora, such as *Bidens* (Gillett and Lim, 1970). In part, these patterns may result from recency of speciation. The fact that species are geographically isolated may also be responsible: Closely related congeneric species in the Hawaiian flora are rarely sympatric.

In general, woody genera tend to develop interspecific barriers to a lesser extent than do herbaceous species (e.g., *Pinus*, *Quercus*). This is related not to woodiness per se but to the fact that woody plants must cope with greater ecological diversity (e.g., plants with deep root systems encounter a greater range of soil structure and soil moisture regimes), and therefore successful occupancy of a diverse area may be related to retention of interspecific fertility, resulting in a more heterogeneous gene pool. A higher proportion of Hawaiian plant species are more woody than are Californian plant species. One key group in which interspecific fertility is widespread (not analyzed in this book) is *Metrosideros* (Myrtaceae), chief tree of Hawaiian forests. As the specific epithet (*polymorpha*) originally given to all members of this complex suggests, the patterns of variation in Hawaiian *Metrosideros* involve the kind of diversity that active hybrid swarms exhibit, but some highly distinct populations have also been recognized as segregate species. Is this confusing pattern the result of

several colonizations of the Hawaiian chain, or even recolonizations within the chain, with subsequent hybridization among the various populations? Certainly, *Metrosideros* represents a remarkably successful system for occupancy by a tree species of various regimes from new dry lava to high bogs and deserves study. When we understand the genetics of *Metrosideros*, we likely will better understand the significance of genetic systems of other Hawaiian plants.

PERSPECTIVES FOR CONSERVATION AND FUTURE RESEARCH

One of the indirect messages contained in this book regards the conservation status of Hawaiian organisms. Information about endangered organisms is a key to their preservation. At first glance, this statement seems to imply that if we know more about a plant or animal, we will know facts that can help us to manage its survival better. That is likely true, but I am also concerned with putting information about endangered species in the hands of the public—simple, appealing facts they can associate with the name of a plant or animal. Information of this sort is essential to public support of conservation efforts, because *the public supports conservation of plants or animals about which it knows something*. Species about which the public knows nothing or about which the public has no visual image are unlikely to be conserved. Therefore, the tremendous amount of information on Hawaiian groups in this book is of great potential value to conservation, and any future efforts to familiarize the public with the unique characteristics of Hawaiian biota are likely to have importance in gaining support for conservation efforts.

Conservation efforts may or may not succeed in saving any particular Hawaiian species, regardless of how intensive those efforts may be. Faced with this, our best option other than continuation of conservation efforts is to study Hawaiian species intensively. Future generations may not fault us for failure to save a species that could not have been saved with reasonable, simple, practical measures. They will surely fault us, however, if simple measures were available but not used and may, justifiably, fault us for not gathering as much information (especially information that can only be gathered from living specimens) as we can while these species are still in existence. Authors in this book have made enormous contributions toward the goal of advancing our store of knowledge of Hawaiian organisms and are to be commended.

2 Geology and Biogeography of the Hawaiian Islands

HAMPTON L. CARSON AND
DAVID A. CLAGUE

The diverse biota of the Hawaiian archipelago presents a large number of geographic puzzles. Many forms have continental affinities, but these oceanic islands are among the most isolated in the world. The most challenging questions deal with origins. Where did each of the many endemic terrestrial immigrant lines and species come from? When did they, or their ancestors, arrive? Are they aboriginal products of evolution that has occurred in situ on the present islands or were they bequeathed, essentially unchanged, from nearby ancient land masses that have since disappeared? Whatever the answers, the ancestral lineages that have led to the present-day endemic species need to be identified genetically. This process is now possible through the use of exquisite new techniques that use molecular markers of ancestry.

Beyond these phylogenetic problems, there is another and even greater challenge. We may look at the population genetics of selected island forms and try to identify the proximate causative factors that have promoted evolutionary character change in their populations. Populations that have colonized the recent lava flows of the newer islands deserve special attention as possible sites of dynamic genetic change.

To provide a background to these studies, we review geologic and geographic information that provides the time and spatial control for investigating further these challenging lines of inquiry, building on several other compilations and reviews that have dealt with Hawaiian biogeogra-

phy (Zimmerman, 1948; Kay, 1972; Carlquist, 1980) and geology (Clague and Dalrymple, 1987).

HAWAIIAN ISLANDS AND PLATE TECTONICS

Unique new data exist on the geologic history of the Pacific, the greatest of the earth's oceans. Plate tectonics has revolutionized our understanding of the "ring of fire" that fringes the Pacific and of the many mid-Pacific islands. This volume focuses on the biological history of one such group, the Hawaiian archipelago. The geologic data permit us to formulate more realistic interpretations of both the biogeography and evolutionary patterns of the organisms present. The implications discussed here deal particularly with terrestrial biota but are also relevant to marine organisms.

Thirty years ago, J. Tuzo Wilson (1963) proposed an insightful new hypothesis to explain the origin of the Hawaiian Islands. This is now the main unifying theory for the origin of many oceanic island groups worldwide (e.g., Christie et al., 1992). Simply stated for the Hawaiian Islands, the evidence indicates that the islands were formed successively over a fixed "hot spot" beneath the northwestward-moving Pacific tectonic plate. Morgan (1971) provided a physical model that consists of a thermal plume of material arising from the deep mantle that forms a melting anomaly beneath the plate. The magma perforates the plate at intervals to form discrete volcanoes as the plate slowly moves over the hot spot. The highest points may rise above sea level as emergent oceanic islands.

The eight current high islands of the archipelago occupy the southeast end of a much longer and remarkably straight line of low islands and seamounts, the Hawaiian Ridge, extending 3,493 km northwest of Kilauea to Daikakuji Seamount (Figure 2.1). At this point, the orientation of the chain turns sharply northward and, known as the Emperor Chain, continues for another 2,327 km, culminating at Meiji Seamount. The latter may have resulted from the initial volcanic activity over the Hawaiian hot spot about 75 to 80 million years ago (Ma). Although the rate of movement of the Pacific plate has apparently undergone occasional slight changes, the direction of movement shifted dramatically from north to northwest about 43 Ma. This shift in direction is now marked by the Hawaiian-Emperor Bend (Figure 2.1). Since the time of the bend, the Pacific plate has been moving 8 to 9 cm/year over a fixed hot spot located at about 19° N, 155.5° W (Clague and Dalrymple, 1987).

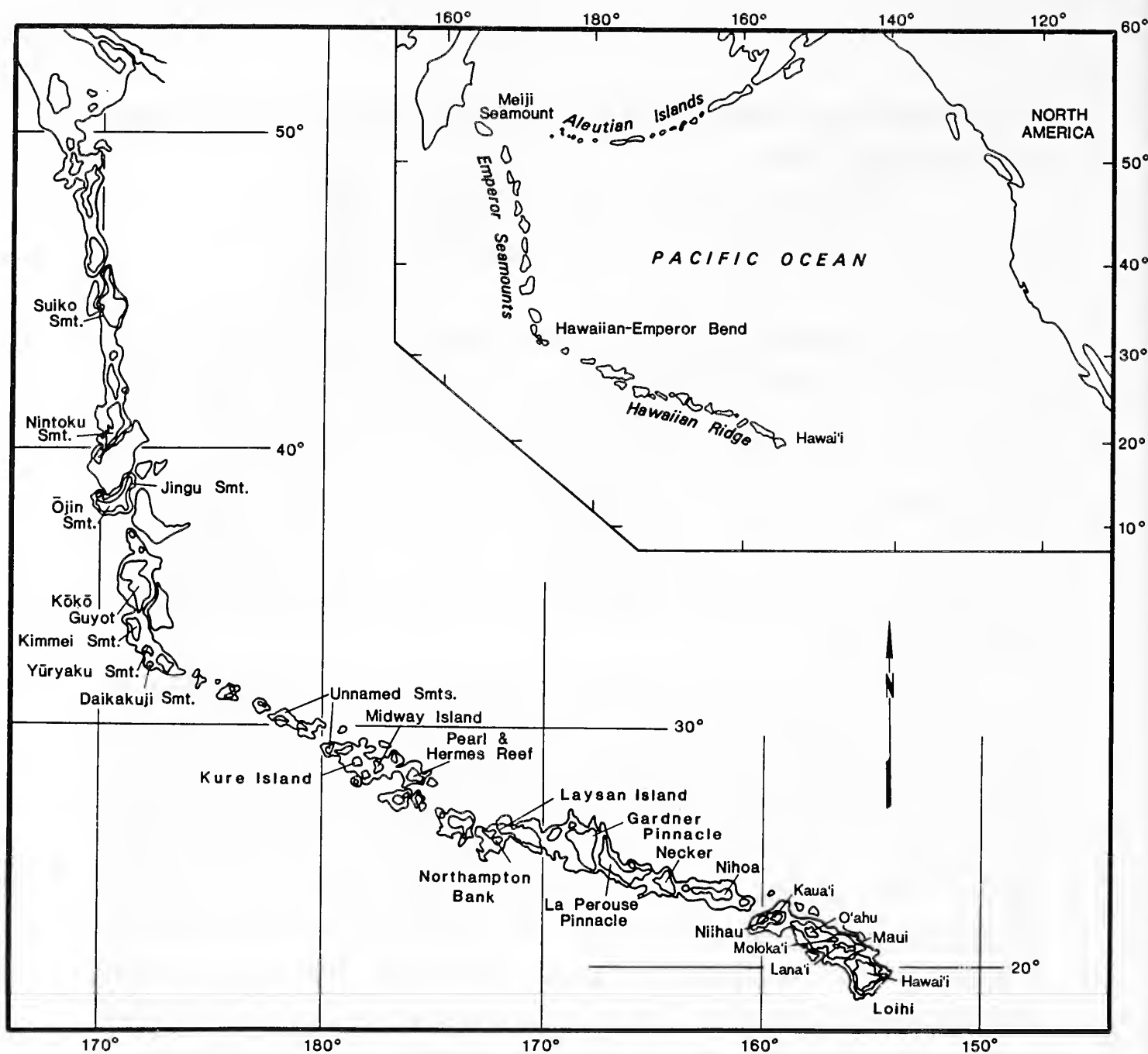


FIGURE 2.1. Bathymetry of the Hawaiian-Emperor volcanic chain. Contours at 1-km and 2-km depths shown in area of chain only. *Inset:* Location of chain, outlined by 2-km depth contour, in central North Pacific. From Clague and Dalrymple (1987).

Each Hawaiian volcanic island and submerged seamount in the Hawaiian-Emperor Chain (Figure 2.1) appears to have been formed in succession; all continue to drift northwestward on the surface of the Pacific plate. This process has produced a series of islands, each of which is younger than its neighbor to the northwest. Of the eight high Hawaiian Islands (i.e., more than 400 m above sea level), Kaua'i in the northwest is the oldest, formed about 5.1 Ma. As diagrammed in Figure 2.2, this age corresponds to the time when the island of Kaua'i was directly above the

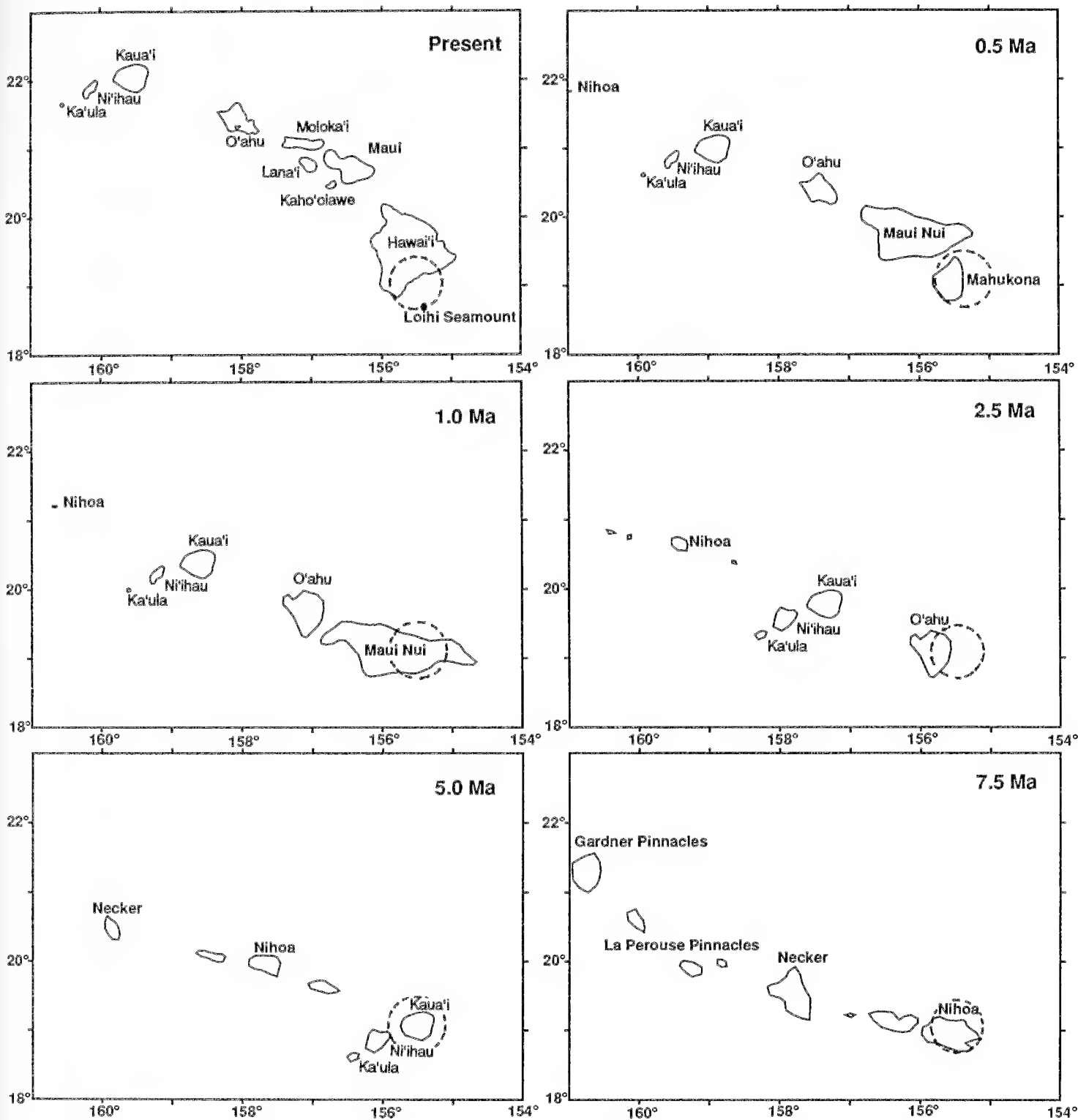


FIGURE 2.2. Coordinate positions in the Pacific Ocean of the present Hawaiian Islands and their reconstructed positions at five different times in the past, as affected by the movement of the Pacific plate. The rate of movement of the plate is assumed to be 9 cm/year. In each panel, the Hawaiian hot spot is indicated (*light dashed circle*) and lies at approximately 19° N, 155.5° W. Islands, ridges, and reefs are identified by outlines; their sizes and fused state at the earlier times are estimates based on bathymetry and GLORIA side-scan data.

Hawaiian hot spot. The southeast portion of the island of Hawai'i, which includes the three active volcanoes Mauna Loa, Kilauea, and Hualalai, now sits above the hot spot. Lo'ihi Seamount is a new active volcano on the southeast flank of Mauna Loa about 30 km offshore; it rises to within 950 m of sea level (Figure 2.2, upper left). Potassium-argon ages and paleomagnetic declination measurements confirm the recency of the island of Hawai'i; no lava flows formed earlier than about 0.5 Ma have been found (McDougall and Swanson, 1972).

HIGH AND LOW ISLANDS

The height of the islands relative to sea level is inevitably reduced by two factors, erosion and subsidence. The greatest elevations above sea level are currently displayed by the islands at the southeast end of the archipelago; they decline in height to the northwest. For example, Mauna Kea rises to 4,205 m, whereas the highest points on Maui, O'ahu, and Kaua'i are 3,055, 1,231, and 1,598 m, respectively. Farther to the northwest, the elevations are low in comparison; examples include Ni'ihau, 390 m; Nihoa, 277 m; Necker, 84 m; Laysan, 11 m; Midway Atoll, 3.7 m; and Kure Atoll, 6.1 m. In the latter three, the volcanic rocks are well below sea level. Kure Atoll is the northernmost island; the westernmost Hawaiian Ridge and the entire Emperor Chain are currently submerged.

The Hawaiian Islands to the northwest of Kaua'i have relatively sparse terrestrial biotas that nevertheless appear to include some recent relict species (Conant et al., 1984). It seems hardly possible that propagules arising from these low islands could be a source of a significant number of suitable colonists for the higher-altitude areas of the newer islands. The extraordinary diversity, specific and generic endemism, and discordant nature of these high-island biota require further explanation, as discussed below.

Many volcanoes of the Hawaiian-Emperor Chain were at one time high islands. Direct evidence as to how high they were and what the nature of their terrestrial biota might have been, however, is lacking. Estimates of their former height have been made based on their shore lines identified using bathymetric and GLORIA side-scan data (Torresan et al., 1991) and the slopes of the currently active volcanoes (see island outlines in Figure 2.2). These volcanoes, at the time they were high islands, were located near the position of the present high islands. Plate tectonic reconstructions (e.g., Atwater, 1989) further indicate that the

islands were probably just as remote from the continents fringing the Pacific as are the modern islands.

DEVELOPMENT OF THE HAWAIIAN ISLANDS

All the volcanoes in the Hawaiian Islands, with the exception of Lo'ihī, Kilauea, and Mauna Loa, were once significantly higher than they are at present. Moore and Clague (1992) estimated the maximum heights that the volcanoes from O'ahu to Hawai'i once attained by adding the current height above sea level and the depth of the deepest slope break below sea level (former shoreline). Their results are shown in Table 2.1, with additional estimates for several older volcanoes in the chain; potassium-argon ages for each volcano are also given. As the volcanoes subsequently grew, many coalesced to form composite islands, and as these islands then sank, they once again became separate islands made of one or more volcanoes. For example, Kaua'i and Ni'ihau formed as two separate islands that coalesced as Kaua'i grew, but later they separated to become separate islands once again as they subsided. The wide and deep Kaua'i Channel between Kaua'i and Wai'anae volcano on O'ahu provided a formidable hurdle to species migration along the chain. However, the channel was not nearly as wide as it now appears because the Ka'ena Ridge to the northwest of Wai'anae volcano was a subaerial ridge when it formed at perhaps 3.5 Ma. Thus, the channel between Kaua'i and Ka'ena Ridge was only about 48 km across, compared with the 116-km width of the present-day channel.

In contrast, for the subsequent volcanoes to form, after Wai'anae and until Haleakala, each coalesced with the previously formed volcano. The channel between Ko'olau and Penguin Bank is only 690 m deep, yet the islands have subsided more than this (1,100 to 1,200 m), so these volcanoes were once joined above sea level with a minimum elevation of about 400 m. Similarly, volcanoes that comprise the Maui Nui complex, which consists of East and West Maui, eastern and western Moloka'i, Lana'i, and Kaho'olawe, were at one time joined by land bridges with minimum elevations of 1,300 m. The large Maui Nui complex first became two islands, one consisting of Moloka'i and Lana'i and a second consisting of Maui and Kaho'olawe. This breakup happened less than 300 to 400 thousand years ago (ka). Kaho'olawe then separated from Maui and finally Lana'i separated from Moloka'i, both less than 100 to 200 ka. It is unclear when Penguin Bank subsided to sea level, as the coral cap is of unknown

TABLE 2.1. Present and Maximum Heights and K-Ar Ages of Hawaiian Volcanoes

| Volcano | Height (m) ^a | | Age (millions of years) ^c |
|------------------------------------|-------------------------|----------------------|--------------------------------------|
| | Present | Maximum ^b | |
| Lo'ihi | -950 | -950 | No K-Ar data |
| Kilauea | 1,247 | 1,247 | 0-0.4 |
| Mauna Loa | 4,169 | 4,169 | 0-0.4 |
| Mauna Kea | 4,205 | 4,600 | 0.38 |
| Hualalai | 2,521 | 2,950 | See Fig. 2.3 |
| Kohala | 1,670 | 2,670 | 0.43 |
| Mahukona | -1,100 | 235 | See Fig. 2.3 |
| Haleakala | 3,055 | 5,000 | 0.75 |
| Kaho'olawe | 450 | 2,100 | 1.03 |
| West Maui | 1,764 | 3,400 | 1.32 |
| Lana'i | 1,027 | 2,200 | 1.28 |
| East Moloka'i | 1,515 | 3,300 | 1.76 |
| West Moloka'i | 421 | 1,600 | 1.9 |
| Penguin Bank (21° N, 157°35' W) | -200 | 1,000 | No K-Ar data |
| Ko'olau | 960 | 1,900 | 2.6 |
| Wai'anae | 1,231 | 2,220 | 3.7 |
| Kaua'i | 1,598 | 2,600 | 5.1 |
| Ni'ihau | 390 | 1,400 | 4.89 |
| Ka'ula | 168 | 800 | 4.0 |
| Unnamed (22°40' N, 161° W) | -200 | 800 | No K-Ar data |
| Nihoa | 277 | 1,300 | 7.2 |
| Necker | 84 | 1,100 | 10.3 |

^aNegative values represent meters below sea level (submarine volcanoes).

^bFrom Moore and Clague (1992).

^cBest K-Ar data on surface basalt (from Clague and Dalrymple, 1987).

thickness. However, we assume that it separated from West Moloka'i before Moloka'i and Maui became separate islands.

The channel between Haleakala and Kohala volcanoes is 1,890 m deep, and subsidence on the south side has been on the order of only 1,000 m. Therefore, Maui and Hawai'i never had a land bridge between them, and species had to cross a narrow channel. The subsided shorelines on the two sides of the channel are only about 13 km apart, so the channel was this narrow when Kohala formed a high island about 370 ka (see also Figure 2.3).

EROSION

Erosion is an important process that reduces a new high island to sea level. At the latitude of present-day Hawai'i, the persistent northeast trade winds and the southerly "Kona" winds are heavily laden with moisture that, as rain, brings about surface erosion.

Catastrophic collapses of large sections of the present islands have been identified by systematic submarine mapping of the Hawaiian Ridge between Kaua'i and Hawai'i (Moore et al., 1989; Moore et al., 1994). Slump and avalanche debris deposits are exposed over approximately 100,000 km² of the ridge and adjacent sea floor or an area more than five times the surface area of the present islands. These slope failures begin before emergence of the island and continue after emergence and after dormancy. Seventeen such deposits have been recognized around the present-day high islands, involving areas adjacent to each. Examples for the island of Hawai'i are diagrammed in Figure 2.3. The data indicate that these collapse events are a normal part of the cycle of island growth and decline.

Such large landslides could affect biogeography by removal of certain gene pools or even localized species. Further, they might be instrumental in introducing species from one island to another by rafting of debris after the slide has occurred.

SUBSIDENCE

Many data show that large volcanic islands sink below the ocean surface. Subsidence, however, is not a linear process but occurs in two distinct stages (Moore, 1987). The most rapid sinking comes about when a large volcano is still in an active state of growth. This early phase results from the flexure of the underlying plate caused by the added load of the volcano. The island of Hawai'i, for example, is currently subsiding at rates of at least 2.5 to 3 mm/year and has been for the past 0.5 million years. Within 1 million years, the subsidence slows dramatically. A second slower phase of subsidence is mainly due to thermal contraction as the lithosphere ages with increasing distance from the hot spot. Observations indicate that subsidence of Maui, O'ahu, and Kaua'i, for example, is currently much slower than that of Hawai'i. Although this process continues for tens of millions of years, the rate decreases so that nearly all the subsidence occurs in the first 10 to 20 million years. By the time the seamounts are 40 to 50 million years old, they are subsiding only very slowly.

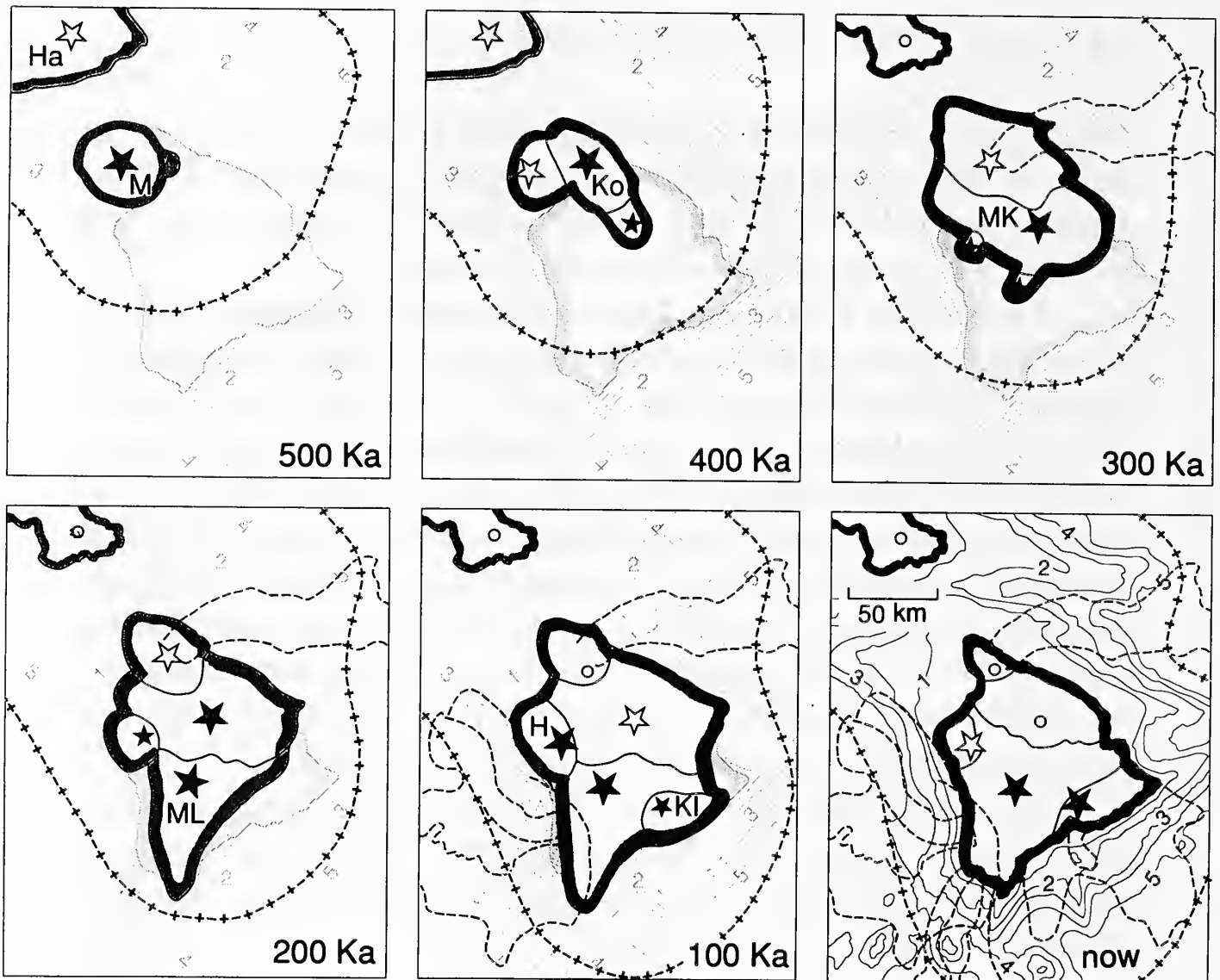


FIGURE 2.3. Six stages in the growth of the island of Hawai'i over the past half-million years on present-day base map. Existing bathymetric contours are shown by *fine lines* (depth in km). Island growth is shown at 100-ka intervals (**bold numbers**), with shoreline and volcano boundaries (**heavy solid lines**), vigorous subaerial volcanic centers (**solid stars**), waning subaerial volcanic centers (**open stars**), dormant or feebly active subaerial volcanic centers (**open circles**), axis of Hawaiian Deep (**cross-dashed line**), and boundaries of landslides (**stippled pattern delineated by dashed lines**). The shorelines are mapped as a break-in-slope offshore of the present coast and are inferred where buried by growth of subsequent volcanoes. Volcanoes (delimited by lines within island) are Ha, Haleakala; M, Mahukona; Ko, Kohala; MK, Mauna Kea; ML, Mauna Loa; H, Hualalai; Kl, Kilauea. From Moore and Clague (1992).

LIFE HISTORY OF A PACIFIC OCEANIC ISLAND

Separating the dual but basically parallel influences of erosion and subsidence of oceanic islands has been possible only with sophisticated new technology that involves deep-sea drilling and sonic imaging. Variations

in sea level further complicate the picture, although this is a small effect compared with subsidence. From the perspective of the terrestrial biogeographer, however, the important point in this discussion is the gradual northward motion and reduction to sea level or below of former volcanic oceanic islands that once may have had an abundant and diverse terrestrial biota.

Such islands may be viewed as having a motion like that of a conveyor belt. The island is constructed by active volcanism and, before moving away from the hot spot, may attain substantial mass and altitude. For a period of several million years, more or less, each new island can serve as an active substrate for colonization and diversification. Propagules may arrive by long-distance dispersal but are more likely to come from an adjacent older island. In the Hawaiian Islands, one may visualize the island chain in motion toward the northwest and most of the colonists moving southeast, in the opposite direction. As the island moves away from the source of magma, it becomes more stable biologically. At middle age, it may approach a biogeographic equilibrium of colonization and extinction in the manner proposed by MacArthur and Wilson (1967). Following this, as the island is further reduced by erosion and subsidence, this equilibrium will become perturbed and the overall biota gradually reduced by extinctions for which colonizations can no longer compensate. As old age sets in and the island approaches sea level, the diversity of terrestrial species would be expected to slowly become depauperate before submergence is complete. This is true for the Hawaiian archipelago because of its northerly location, which is marginal for coral growth. Other islands in more equatorial locations should become atolls that persist for long periods (e.g., the Marshall Islands). All such islands eventually end up below sea level. This view of the eventual fate of an oceanic island calls for a revision of the MacArthur-Wilson equilibrium theory, as suggested by McKenna (1983) and Carson (1992a).

From data on the distribution of coral reefs, Darwin (1837) deduced that the subsurface platforms and seamounts in the Pacific were sunken islands. Modern study of the guyots of the western Hawaiian Ridge and Emperor Seamounts confirms these ideas, which have also been applied to seamounts found on the easternmost portion of the Galápagos Ridge (Christie et al., 1992). The implications of subsidence for the distribution of marine life, as Darwin recognized, are very great, because a sinking island in tropical waters acquires coral reefs. The main effect, however, is an irreversible loss of terrestrial life.

TERRESTRIAL BIOTA OF THE PRESENT HIGH HAWAIIAN ISLANDS

The diversity of the highland biota of the modern high Hawaiian Islands is surely one of the wonders of world biogeography. The importance of the rapid rise and eventual subsidence of islands for the interpretation of island biotas can hardly be overestimated. If the Hawaiian Islands and their biota are viewed wholly from the perspective of their present geographic position, the biogeographer may overlook the northwestern low islands and assume that the progenitors of any endemic or indigenous biotic element must have arrived in Hawai'i from fringing continents or distant island sources. Furthermore, the surface of the present high Hawaiian Islands is geologically youthful (i.e., no older than 5 to 6 million years), so that the recency of the unique living species is indeed striking, no matter where the founding propagules came from.

A case can be made for some recent (i.e., less than 5 Ma) colonization by propagules from remote continental sources. With the advent of the use of molecular markers, this possibility can be tested; examples are presented in this volume. Nevertheless, the ancient high islands of the Hawaiian-Emperor Chain need to be considered as a source of propagules for at least some of the immigrant lines found on the present Hawaiian Islands.

As has been indicated earlier, the endemic terrestrial biota of the present low Hawaiian Islands is depauperate compared with that of the high islands (Table 2.2), so that one cannot realistically search the present

TABLE 2.2. Approximate Numbers of Endemic Species in the Terrestrial Biota of the High and Low Hawaiian Islands

| Taxon or island characteristic | Southeast High Islands (Kaua'i to Hawai'i) | Northwest Low Islands (Nihoa to Kure Atoll) |
|------------------------------------|---|--|
| Insects | 2,300 | 50 |
| Land snails | 1,000 | 8 |
| Land birds | 70 | 4 |
| Ferns and allies | 120 | 0 |
| Flowering plants | 850 | 12 |
| Total | 4,340 | 74 |
| Area (km ²) | 16,576 | 8.29 |
| Endemic species/10 km ² | 38 | 1 |

biota of the low islands for clues to the origin of endemic high-island forms. Direct evidence, however, exists of ancient terrestrial biota. This has been obtained from cores that were drilled as part of the Deep Sea Drilling Project. In 3 of 46 samples taken from 20 cores from leg 55 of this project, Koreneva (1980) reported single spores of the fern families Pteridaceae, Schizaeaceae, Cyatheaceae, and Polypodiaceae, two pollen grains belonging to conifers of the gymnosperm family Pinaceae, and one pollen grain from an angiosperm. This material was obtained from hole 433B, drilled in Suiko Seamount in the Emperor Chain. This volcano was determined to have a potassium-argon age of 64.7 million years (Dalrymple et al., 1980). Although this evidence appears to support the theory that substantial islands with fernlike vegetation existed as long ago as the Paleocene, the possibility exists that these spores and pollen grains may have arrived by long-distance dispersal. A rain of conifer pollens and fern spores over great distances, including oceans, is well known (McDonald, 1962; Hirst et al., 1967).

OLD LINEAGES AND NEW SPECIES

High-altitude islands have existed in the present position of the Hawaiian Islands much of the time since the late Paleocene. To what extent did such islands harbor biota that contributed in some way to that of present-day, high-altitude Hawaiian Islands? In considering this question, a distinction must be made between immigrant lines of descent (lineages) and species that have evolved in situ (autochthonous species). A line of descent of present-day organisms may be traced back many millions of years (indeed perhaps to the Precambrian!), but at any one time, it consisted of a series of distinct species. These are basically genetically variable populations living under natural selection. Long-surviving individual species that have remained unchanged over geologic time ("living fossils"), if they indeed exist, are likely to constitute only a small fraction of the total biota.

When we examine the present-day terrestrial biota of the archipelago, species endemism is very high. Many organisms form clusters of phylogenetically closely related species. These clusters often have representatives on all or most of the present islands.

In many cases, the individual species that make up these phylogenetic clusters are found to be endemic to one island or even to individual volcanoes. The conclusion is usually drawn that such endemic species have newly evolved in situ since the island or mountain was formed. An

alternative theory, vicariance, holds that these species might have completed the speciation process on an older island that, with its biota, has since disappeared. Accordingly, this view contends that a species observed at the present day might be considered to represent a taxon that is a basically unchanged descendent from these older forms. This might, in turn, lead to the conclusion that the species is older than the island on which it is found. High species endemism on the present islands speaks against the vicariance view, as will now be discussed. At least some of the immigrant lines are relatively old, but the high degree of species endemism suggests rapid and autochthonous speciation within these immigrant lines.

ENDEMISM IN THE HAWAIIAN ISLANDS

A very large number of species have been accidentally or purposefully introduced into the Hawaiian Islands since the arrival of Polynesians about 2,000 years ago and Europeans a few hundred years ago. Most of these species are recognizable as recent introductions and would generally be excluded in a biogeographic study to concentrate attention on the species that arrived before humans. Although a necessary process for the identification of the endemic biota, disregarding human introductions fails to address an interesting problem in the dynamics of evolutionary change. Thus, it is possible that significant genetic changes may have occurred in their populations during the few hundred years since modern introduction. How rapidly can evolution of new species and character sets occur? This is an unexplored problem that greatly needs attention from the population geneticist.

After eliminating the introduced species, one is left with the elements of the biota that are either indigenous or endemic (see discussion by Carson, 1987a). The former designation characterizes species that colonized without the intervention of humans and live naturally in the archipelago as well as in some other place or places. Some of these indigenous species are strand or shore organisms that have wide distributions in the Pacific, being somewhat comparable with certain widespread marine organisms. Of greater significance, however, are the species or genera that are endemic (i.e., entirely restricted to the present islands and not naturally found elsewhere). In the Hawaiian biota, high levels of endemism occur in many groups of related species; in insects, for example, more than 90% of the species are endemic.

The vicariant explanation does not fit well in the case of approximately 100 intensively studied picture-winged *Drosophila* species (Carson and Kaneshiro, 1976; Carson, 1983a, 1990a; see also Kaneshiro et al., this volume, Chapter 5). These species are all endemic to the existing high islands. With only a few exceptions, tracing by the use of chromosomal markers indicates that a succession of new single-island endemic species have evolved as each new volcano and island has been formed to the southeast of an older one. A similar pattern of evolution is shown by plants of the Hawaiian silversword alliance (Asteraceae, Madiinae) on which comparable crucial genetic data have been obtained (Carr et al., 1989; Baldwin et al., 1991). In both cases, although the bulk of the colonizations has been from an older island to a newer one, colonizations in the reverse direction have also been recognized.

The reliability of phylogenetic information provided by specific genetic markers, however, tends to be negatively correlated with the length of time since the cladistic event. In the case of the picture-winged *Drosophila* and the Hawaiian silversword alliance, all species on the newer islands may be traced back genetically to species still existing on Kaua'i, the oldest high island. This does not mean, however, that a continental ancestor of the observed line of descent must necessarily have originally colonized Kaua'i, an island formed 5.1 Ma. Ancestral forms may have colonized the present archipelago by way of an older eroded island. Such an event is indicated by molecular studies of the relationships of some present-day forms. Although the picture-winged flies seem to form a very recently evolved group of species, a closely related group of *Drosophila* species that breed on fungus, also endemic to the islands, have DNA sequences that diverged from the picture-winged group about 10 Ma, twice the age of Kaua'i (Thomas and Hunt, 1991). These authors suggested that the divergence between the fungus feeders and the picture-winged group could have occurred on an island such as 10 million-year-old Necker, which is now reduced to the point that it does not support any *Drosophila* species.

SOURCES OF PROPAGULES FOR THE HIGHLAND HAWAIIAN BIOTA

Although the vicariance idea has its advocates (see Melville, 1981), distributions interpretable as vicariant are infrequent in the terrestrial biota of the Hawaiian Islands. The present biota appears to trace to waifs

(Wagner et al., 1990). All such founding waifs, however, have not necessarily come directly from the distant continents. With proper genetic markers, we may ultimately be able to recognize two kinds of waifs: those originating on the continents or distant islands, and those that were derived from pre-existing, but now-foundered older islands.

Propagules from older islands in the chain were probably not continuously reaching newer islands. After the formation of Koko volcano in the southern Emperor Chain about 48 Ma, no islands higher than 1,000 m formed until Kure about 29 Ma. By the time Kure formed, all the previous high islands had subsided. Thus, there was at least one time in the past when there was no possibility to derive propagules from a previous island (which was already an atoll with depauperate biota) and the entire process of introducing waifs from far away would have restarted. Before the time of the Hawaiian Bend, the volcanic islands, with a few exceptions, were high for only a short time, and it is possible that the process of colonization from older to younger islands was cut off several times during the Paleocene and Eocene.

The isolation of the Hawaiian-Emperor Chain is so great that one must look to the fringing continents and other island groups as the ultimate source of the biota by long-distance dispersal (Carlquist, 1980). Data on the wide dispersibility of many of the immigrant lines of the Hawaiian biota (e.g., Fosberg, 1963; Gressitt and Yoshimoto, 1963) reinforce this view, and there is reason to believe that propagules from the continents have continually played a role in both ancient and modern times. Moreover, some of the island groups in the Pacific (e.g., Fiji) might have served as "stepping stones" for immigrant lines from more remote islands or continents. There is no evidence, however, for the existence of any "lost" or sunken mid-Pacific continents. Rotondo et al. (1981) cite the existence of two older seamounts near Necker and Kure atolls. They suggest that these could have contributed to the Hawaiian biota. However, this seems unlikely because these seamounts were not islands at the same time as any nearby Hawaiian islands.

The question becomes one of deciding from where and how long ago arrival in the Hawaiian-Emperor Chain took place. With molecular methods, precise identification of putative ancestral stocks for groups and species is now possible. Each immigrant group of interest needs to be separately examined from this point of view. If carefully applied, molecular methods for estimating time since divergence should provide hard data indicating when such an event occurred.

ISLAND OF HAWAI'I—A PARADIGM OF "MICROBIOGEOGRAPHY"

Hawai'i Island is both very large and very young. It also contains many species and sets of characters that are endemic to this island alone. The biogeographer may thus use the species of this island as examples of dynamic and recent evolutionary process on a relatively small geographic scale (Carson, 1983b; see also DeSalle, this volume, Chapter 6). Molecular markers such as mitochondrial DNA (mtDNA) can provide historical data of extraordinary interest even for different populations of a single species, a field that has been called *intraspecific phylogeography* (Avice et al., 1987).

The newness of Hawai'i Island has permitted a detailed geologic reconstruction of its development through a succession of volcanoes of varying very recent ages. Moore and Clague (1992) have traced the origin of the present five volcanoes of this island from their beginnings about 0.5 Ma, using ancient shorelines (Figure 2.3). Mahukona volcano reached its largest size about 465 ka, Kohala 245 ka, Mauna Kea 130 ka, and Hualalai 130 ka. The picture is completed by including the currently active and very recent Mauna Loa and Kilauea. In view of these new data, the opportunities for tracing and timing the recent evolution and colonizing history of selected indicator organisms with great accuracy are unparalleled.

Even beyond the biogeographic situation, it has been suggested that genetic shifts and formation of new character sets and species may be most active at the time a new shield volcano is growing (Carson et al., 1990). Single founder events of one or a few sexual propagules that are followed by immediate expansion of the new population to a large size do not appear to necessarily result in inbreeding depression or loss of significant quantitative genetic variability from the new population (see review by Carson, 1990b).

The rise and fall of islands in an extended succession, back at least as far as 65 Ma, appears to have elicited continued novel evolution mediated by stepwise founder effects separated by periods of expansion of population sizes. Many different lines of descent appear to have been affected by such events in a similar manner, indicating that many organisms have the capacity to retain extensive genetic variability despite occasional bottlenecks of population size.

3 Cladistic Methods

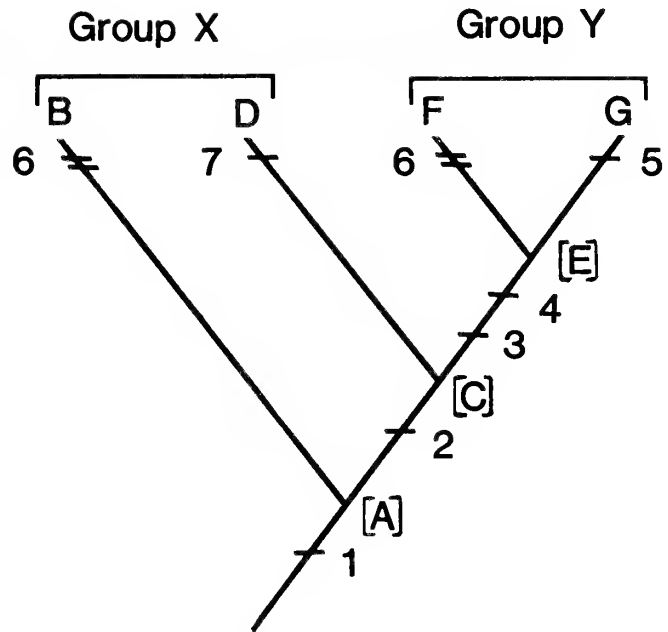
V. A. FUNK

The authors in this volume have used the methods of phylogenetic systematics, also called cladistics, to develop phylogenies and examine monophyletic groups (referred to as *clades*)¹, in a rigorous way. Thorough explanations of cladistics can be extremely complex. This discussion is not intended to be comprehensive; rather it is an introduction to the concepts and terminology necessary for the reader inexperienced in phylogenetic theory to understand the analytic aspects of the chapters in this volume. Additional discussions can be found in Hennig (1966), Nelson and Platnick (1981), Wiley (1981), Swofford and Olsen (1990), Wiley et al. (1991), Forey et al. (1992), Maddison and Maddison (1992), Swofford (1993), and references cited therein.

Cladistics seeks to answer the following question: Given any group of more than three taxa, which taxa are more closely related to one another than to any other taxa? Relatedness is identified by the sharing of one or more uniquely derived characters that other taxa outside the group do not possess. For example, within vertebrates the unique derived character “feathers” identifies all birds as being most closely related to each other. The branching pattern of the tree that illustrates this relatedness is formed by the distribution of the unique characters in the way that

¹Most of the clades identified in this book do not have formal taxonomic names and, for emphasis, are given in italics and without capitalization (unless derived from a proper name).

FIGURE 3.1. Cladogram. Letters represent taxa, whereas letters in brackets are hypothetical ancestral taxa. Numbers represent apomorphic characters of the transformation series; those with *single bars* are apomorphic, and those with *double bars* are independently derived. Group X is paraphyletic, a grade. Group Y is monophyletic, a clade.



requires the least amount of convergent or parallel evolution and character loss. A tree formed solely by these unique characters can be called a *cladogram* but is also called a *phylogenetic tree* or *tree* (Figure 3.1). Cladograms are characterized by the fact that their information is contained in the branching sequence and not in the physical proximity of the terminal branches. For instance, Figure 3.2 shows the same branching sequence as Figure 3.1, and as far as information content is concerned, it is identical. In Figure 3.1, B is next to D, but in Figure 3.2 B is next to F. Neither of these physical locations gives the correct relationship because the branching sequence of both figures shows that the actual relationship is one of B being most closely related to the group of taxa DGF (see discussion on Venn diagrams below). A cladogram in which the branch

FIGURE 3.2. Cladogram with the same branching sequence and the same information content as Figure 3.1.

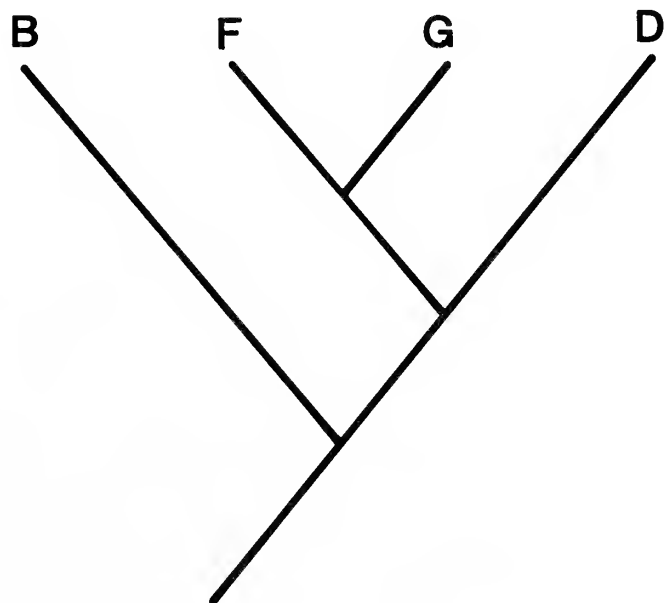


TABLE 3.1. Character Matrix for Figures 3.1 to 3.3

| Taxon ^a | Transformation series | | | | | | |
|--------------------|-----------------------|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| OG | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| B | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| D | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| F | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| G | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| [A] | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| [C] | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| [E] | 1 | 1 | 1 | 1 | 0 | 0 | 0 |

^aB, D, F, G, and the OG (outgroup) are actual taxa, whereas A, C, and E are hypothetical taxa whose character data are inferred from the most-parsimonious tree.

and internode lengths reflect the number of characters on that branch or internode is called a *phylogram*.

Cladistics has as its basis three concepts: apomorphy, monophyly, and parsimony. An *apomorphy* is a uniquely derived evolutionary character. Hennig (1966) called these *apomorphous characters*, but various other permutations of the term now include *apomorphic character* and *apotipic*. There are related terms; for instance, every apomorphy either is found in one taxon, an *autapomorphy* (Figure 3.1, apomorphic characters 5 and 7; Table 3.1), or is shared by more than one taxon, a *synapomorphy* (Figure 3.1, apomorphic characters 1 to 4). A synapomorphic character, in the true sense, is one that has evolved once in the ancestor of a group of taxa marking a common evolutionary history for that group. Every apomorphous character is paired with the character from which it is derived, the *plesiomorphous character* (or *plesiomorphic character* or *plesiomorphy*). In the bird example, “feathers” is the apomorphic character, and because feathers are believed to be derived from scales, then “scales” becomes the plesiomorphic character.

The apomorphic and plesiomorphic characters together form an *evolutionary transformation series* (often abbreviated TS) (Hennig, 1966; Wiley et al., 1991). The transformation series can contain more than one apomorphic character, provided they are evolutionarily homologous. Some authors refer to individual characters as *character states* and transformation series as *characters*, and both systems are used in this book. However, this alternative terminology necessitates placing apomorphic

and plesiomorphic character states into characters rather than transformation series. Unfortunately, users of the term *character state* sometimes incorrectly shift to the term *character* in the discussion section. To be unambiguous, the transformation series concept is preferred.

The terms *apomorphy* and *plesiomorphy* are dependent on their relative position on a cladogram. A character that is synapomorphous at a node when one is discussing group Y (Figure 3.1, apomorphic character 3) will be plesiomorphous if one is discussing the characters that delimit taxon G. When characters are found in more than one taxon, they are considered to be evolutionarily or phylogenetically *homologous* (Patterson, 1982, 1988). If what appears to be the same apomorphic character is found in two unrelated groups, it is considered to be nonhomologous and therefore not a single apomorphy (Figure 3.1, apomorphic character 6) and is referred to as a *homoplasious character*. If a character occurs as a synapomorphy on a cladogram and is subsequently lost in one or more taxa, then it is a *character loss* (also referred to as a *reversal*, but this term can be confused with genetic terminology). Homoplasious characters and character losses may obscure the phylogenetic pattern. These seemingly contradictory characters are referred to as *character conflict*. Such conflicts are resolved by parsimony analysis, and once they are recognized and understood, become apomorphic characters themselves.

The *parsimony* criterion governs how cladograms are constructed. It is nearly identical to Hennig's Auxiliary Principle: "Never assume convergence or parallel evolution, always assume homology in the absence of contrary evidence" (Hennig, 1966, according to Wiley et al., 1991; Farris, 1983). This principle does not preclude the possibility of convergent or parallel evolution; it simply states that when there is no reason to think otherwise, two characters that appear to be the same are treated as homologous. This means that the character has the potential for grouping taxa if it is apomorphous. When characters support conflicting groups (Figure 3.1, apomorphic character 6), the explanation that is the simplest is chosen (i.e., the one that requires the smallest number of homoplasious characters and character loss). Therefore, the user of parsimony is not making any statement about the process of evolution.

A *monophyletic group* is a group of taxa that share a common ancestor and includes all descendants of that ancestor, also referred to as a *clade*. On a cladogram, this translates into any group that includes all taxa that share at least one synapomorphy (Figure 3.1, group Y). Figure 3.3 is a Venn diagram for Figures 3.1 and 3.2; each ellipse represents

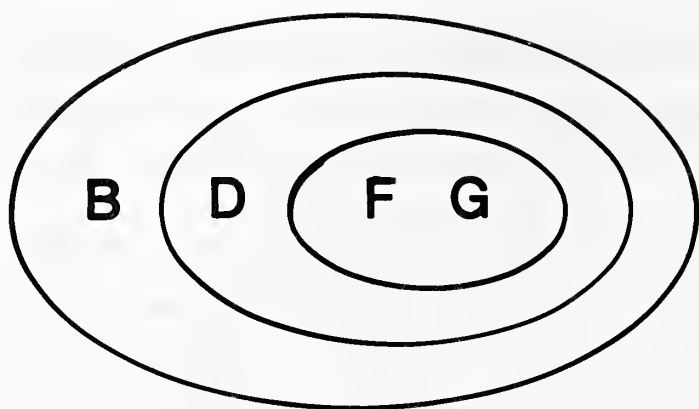


FIGURE 3.3. Venn diagram of Figure 3.1.

a monophyletic group so that one can easily see three such groups, FG, DFG, and the whole clade, BDFG. However, the concept of monophyly is far more than a definition of a group of taxa. Concomitant with it is the notion that the only groups that are evolutionarily meaningful (natural) are monophyletic ones. Therefore, in this view, the only groups that can be recognized in formal classifications are monophyletic ones. The justification for this position lies in the nature of the groups. If groups include an ancestor and all its descendants (monophyletic), then the groups reflect a common evolutionary history and can be used to study speciation, biogeography, pollination biology, and other evolutionary concepts. *Non-monophyletic* groups are of two types (Farris, 1974). In Figure 3.1, A is the ancestor of taxa B, D, F, and G. Group X contains the common ancestor A, but only two of the descendants, B and D, and so it is not monophyletic. Such a group, one that includes some but not all of the descendants (Figure 3.1, group X), is called *paraphyletic*, which is also referred to as a *grade*. *Polyphyletic* groups have been defined several ways, but, in general, they consist of taxa taken from more than one monophyletic group. Under certain circumstances, it is difficult to separate paraphyletic and polyphyletic groups, so often authors simply refer to any group of taxa that does not satisfy the criterion of monophyly as non-monophyletic.

Both monophyly and parsimony depend on apomorphous characters; therefore, apomorphies are the central concept of cladistics. The process of assigning the status of apomorphy to a character is called determining *polarity*. Using an *outgroup* (or outgroups) is the most common way of determining which characters are apomorphic (Watrous and Wheeler, 1981; Farris, 1982; Maddison et al., 1984). Characters found in the outgroup as well as in some of the taxa of the group being studied (the *ingroup*) are considered to be plesiomorphous. Those characters found only in some of the taxa of the ingroup but that are absent in the rest of

the ingroup and in the outgroup are considered to be apomorphous. Many exceptions and extenuating circumstances to be considered when using the outgroup criterion cannot be covered in this brief discussion. Additional information can be found in the general references listed in the first paragraph and in Watrous and Wheeler (1981), Farris (1982), and Maddison et al. (1984). An outgroup can be, but is not necessarily, the taxon most closely related to the ingroup, the *sister group*. In Figure 3.1, DFG is the sister group of B. The outgroup(s) should be a closely related taxon that does not contain large numbers of autapomorphous characters. Sometimes a specific outgroup cannot be identified, and a composite outgroup is constructed by evaluating each transformation series separately to determine which character(s) was apomorphic. Authors in this volume who use this approach have discussed how the composite outgroups were formed. Another method that is occasionally used to assign polarity is ontogeny (Patterson, 1982).

The process of tree construction has changed greatly in the past two decades. Instead of the manual constructing of small character trees for each transformation series, which necessitates examining each character to decide if it is apomorphous and then looking for groups of taxa that can be nested, computer programs are now used. These programs construct networks based on the distribution of shared characters without assigning polarity or evolutionary direction, then root the tree based on the characters present in the outgroup(s), either by using the outgroup(s) as part of the analysis or by attaching it to the network after the analysis is completed. The two most commonly used programs are PAUP (Swoford, 1993) and HENNIG86 (Farris, 1988). These computer programs have increased the speed and accuracy of cladogram production. Moreover these programs have introduced many options that give the user a powerful resource for investigating the phylogeny of the taxa in question. Another program available for analyzing characters and cladograms is MacClade (Maddison and Maddison, 1992), which also has a broad array of options. On occasion, different programs will give different answers to the same questions. It is the user's responsibility to make sure she or he understands and endorses the assumptions that underlie the options in all the programs; otherwise, the results will be misleading (at best) or erroneous.

For years, many phylogeneticists have tried to measure the robustness of data used to construct cladograms, to find a way to assign a value that would indicate how "robust" the cladogram was. The simplest measure is the *tree length*, or total number of *steps*. The tree length is

equal to the total number of characters actually on the tree, including all conflicting characters. The first index, and still the most popular, is the *consistency index* (CI) (Kluge and Farris, 1969). Currently, the index is calculated using only synapomorphies and taking the minimum number of steps necessary if all the data agreed and dividing it by the actual number of steps. The other commonly used index is the *rescaled consistency index* (RC) (Farris, 1989), which multiplies the CI by the *retention index* (RI; ratio of apparent synapomorphy to actual synapomorphy). The RC excludes characters that do not contribute to the “fit” of the tree by excluding autapomorphic characters as well as totally homoplasious ones. The CI and the RC can be used for each individual transformation series (character) as well as the cladogram as a whole. Several other indices have been proposed (e.g., F-ratios, d-measures) (Wiley et al., 1991) but are not used in this volume. Each index has certain strengths and weaknesses, and no one index has been found that really gives us the information we seek, the answer to the question “How good is this cladogram?”

Whereas the indices give information on the tree as a whole (or on the individual transformation series), there is another approach to estimating the value of a particular cladogram with respect to the data and that is by placing confidence limits on the individual branches. Some authors provide such values based on *bootstrapping*. This technique involves randomly sampling with replacement the character information from a data set to build many “bootstrap” data sets of the same size as the original data set, which are then analyzed to give one or more trees. The percentage of occurrences (usually out of 100) that a particular monophyletic group appears among the trees of the sample data sets can be considered an index of support for that monophyletic group. This technique does not result in true confidence limits in a statistical sense. One of the biggest problems is that the values can be related to the size of the data set. Also, it takes three synapomorphies at an internode for a confidence level of 95% to be reached, and these could all be homoplasious characters that occur many times on the tree. There are additional problems with the assumptions required by bootstrapping that can cause either over- or underestimates of confidence (for further discussion, see Sanderson, 1989).

As data sets grow, there is an ever greater chance of the analysis resulting in more than one equally parsimonious tree. A method of working with multiple trees is the implementation of consensus trees (Wiley et al., 1991; Swofford, 1993). Two types of consensus trees are

common in the literature, strict and majority rule. *Strict consensus trees* reflect only the groups that are found in all the equally parsimonious trees. *Majority rule consensus trees* show the branching sequences that are found in most of the trees. Both consensus tree methods have the potential of producing unresolved areas or branching patterns on the consensus tree that are not found in any of the equally parsimonious trees. Although consensus trees are useful in identifying the areas of agreement and conflict among the competing trees, unless a consensus tree is identical to one of the equally parsimonious trees, it cannot be used as a phylogeny beyond the point of agreement found in all trees. For instance, *polytomies* (nodes with more than two branches) that are the result of conflicting branching sequences in competing trees and are not found in any of the competing equally parsimonious trees should not be used as part of the phylogeny. One should consider selecting one of the equally parsimonious trees for use as a phylogenetic tree. Another option for dealing with multiple trees that was used in this book is *successive weighting*, an a posteriori weighting based on the fit of the characters to the trees (Farris, 1989; Swofford, 1993). There are several types of a priori weighting as well, but none were used by the authors in this volume.

When many equally parsimonious trees are produced, especially with molecular data sets, the methods of bootstrapping and majority rule consensus trees are often combined to produce a tree. Extreme caution must be used with such a tree, for there is no way to gauge what relationship it holds with any of the equally most-parsimonious trees.

Once a phylogenetic tree has been produced, one of the most interesting things to do with it is to use it to study evolution. Indeed, the ability to ask questions about evolution is why many researchers are interested in producing phylogenies in the first place. One technique used in this book to facilitate such evolutionary studies is *optimization* or *mapping*. The method is examined in detail in Funk and Brooks (1990), Brooks and McLennan (1991), and Maddison and Maddison (1992); a simplified explanation is offered here. Once a cladogram has been constructed, any feature or condition is selected to be examined in the light of the phylogeny of the group. Examples include habitat, habit, chromosome number, and home range. The condition of each terminal taxon is identified on the cladogram, and hypothetical conditions are assigned to the nodes that reflect the most-parsimonious arrangement of those conditions at each node. This allows one to determine the potential ancestral conditions. In this volume, the method is primarily used to examine

biogeography, but other features examined include speciation and habitat evolution as well as adaptive radiation and coevolution. Of all these features, only biogeography has its own special term: A cladogram in which the terminal taxa have been replaced by their respective distributions is called an *area cladogram*.

Phylogenetic systematics is an interesting, growing, and constantly changing field of study. This brief discussion is an introduction in the hopes that the reader will be able to better understand the chapters in this volume.

ACKNOWLEDGMENTS

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4

Biogeographic Patterns of Two Independent Hawaiian Cricket Radiations (*Laupala* and *Prognathogryllus*)

KERRY L. SHAW

The Hawaiian archipelago is well known to evolutionary biologists for unique biological diversity, particularly for its native insects (Zimmerman, 1948; Howarth and Mull, 1992). Because of the successive emergence of new islands and habitats caused by the northwestern migration of the Pacific plate over a relatively stationary magmatic plume (Stearns, 1985), colonization opportunities are continually created for Hawaiian biota. Compelling evidence exists for a special mode of diversification in some groups such as the native Hawaiian *Drosophila* (Carson and Templeton, 1984) due to this geochronological pattern of island formation. Colonizations from older to younger islands are hypothesized to renew taxonomic diversity and perpetuate the lineage of native *Drosophila* in the Hawaiian Islands, in the face of island subsidence as the islands age and drift to the northwest on the Pacific plate. In other Hawaiian radiations in which enduring and extensive diversity exists, the geologic development of these islands might have a similar effect on the pattern of relationships within those radiations. A phylogenetic frame of reference in concert with knowledge of the geologic history of a region provides a means for inferring the biogeographic history of a group, and this type of analysis is discussed here for a portion of the diverse native Hawaiian crickets (family Gryllidae).

Many attributes of the native cricket fauna make phylogenetic analysis attractive. A relatively thorough treatment of the extant cricket diversity arising from colonizations of the Hawaiian Islands is possible

because it is likely that all taxa arising in the Hawaiian cricket radiations are contained within the archipelago. In species that communicate acoustically, distribution maps are easily compiled because the male calling songs are audible to humans and can often be heard from considerable distances. Furthermore, a general phenomenon of single-island endemism pervades in the native cricket fauna. Perkins (1899, p. 3) noted that "the number of species which fail to extend their range beyond a single island is quite remarkable, more so, I believe, than is the case with any of the other orders of insects." In a recent and more thorough taxonomic investigation of the Hawaiian crickets, Otte (1994) found that all native species except *Caconemobius sandwichensis* are single-island endemics.

Hawaiian crickets are tremendously diverse, both in species richness and in way of life. Among closely related Hawaiian cricket species, the first distinguishable differences tend to be behavioral phenotypes involved in reproduction. Minimally, species hypotheses rely on the differences in the male calling song in groups that possess forewings (Otte, 1994). All native crickets exhibit classic "island flightlessness" (Carlquist, 1980; Williamson, 1981). However, many species retain the forewings (tegmina), which function as male sound-producing organs to which females respond. Only more distantly related species show differences in morphology of the male genitalia, size characters, and pigmentation patterns. Species that do not possess forewings and, therefore, do not sing are described largely on the basis of morphometric differences in the male genitalia.

There have been three substantial and separate radiations into the Hawaiian Islands by the ground crickets (Nemobiinae), the tree crickets (Oecanthinae), and the swordtail crickets (Trigonidiinae) (Otte, 1989, 1994). Like so many other Hawaiian plants and animals (Carlquist, 1980; Simon et al., 1984; Carr et al., 1989), adaptive shifts have occurred within each of these radiations.

The nemobiines include two genera, a widespread Pacific genus, *Thetella*, and the genus *Caconemobius* (with 9 endemic species). *Caconemobius* is noteworthy for adaptive, potentially parallel shifts of lineages into lava tubes from a shore form that inhabits the rocky coastal environment on all the main islands. Cave-inhabiting species, which exhibit eye reduction and a loss of pigmentation, have been discovered on Hawai'i and Maui (Howarth and Mull, 1992; Otte, 1994). Only the *Caconemobius* radiation is most diverse on the youngest islands (Table 4.1). This pattern may result from a loss of rocky and subterranean habitat as the older islands erode and subside.

TABLE 4.1. Taxonomic Diversity by Island in the Endemic Hawaiian Cricket Genera

| Island ^a | No. of species of: | | | | | | |
|---------------------|---------------------|---------------------|-----------------------|-------------------------|--------------------|-------------------|----------------|
| | <i>Caconemobius</i> | <i>Leptogryllus</i> | <i>Thaumtogryllus</i> | <i>Prognathogryllus</i> | <i>Trigonidium</i> | <i>Prolaupala</i> | <i>Laupala</i> |
| Nihoa | 1 | | 1 | | | | |
| Kaua'i | 2 | 3 | 1 | 16 | 27 | | 7 |
| O'ahu | 1 | 7 | | 13 | 34 | 1 | 11 |
| Moloka'i | 2 | 5 | | | 13 | 1 | 1 |
| Maui | 2 | 7 | 1 | 4 | 30 | 1 | 8 |
| Lana'i | 1 | 1 | | | 4 | | 1 |
| Hawai'i | 6 | 5 | 1 | 3 | 27 | | 7 |

Note: All species noted here, except one widespread species of *Caconemobius* are single-island endemics.

^aThere are no known endemic species of crickets on the island of Kaho'olawe.

The tree crickets are represented in the Hawaiian Islands by a radiation that has resulted in three endemic genera: *Leptogryllus* (28 species), *Thaumtogryllus* (4 species), and *Prognathogryllus* (36 species) (Figure 4.1). Perkins (1899) and later Zimmerman (1948) considered these native genera to be closely allied but contained within the Eneopterinae. The presence of tympana on the foretibiae, vestigial forewings, the structure of the metanotal gland, and the male genitalia common to *Thaumtogryllus* and *Leptogryllus* suggest that these genera share a more recent common ancestor than either does with *Prognathogryllus* (Otte, 1994). Members of both *Thaumtogryllus* and *Leptogryllus* hide under bark or in dead leaves and fern fronds close to the ground. Some species of *Thaumtogryllus* live in subterranean habitats or lava tubes, whereas members of the genus *Prognathogryllus* are always found in bushes and treetops. Otte (1994) hypothesized that members of *Prognathogryllus* form a monophyletic sister taxon to *Leptogryllus* and *Thaumtogryllus*. Species diversity in *Prognathogryllus* is generally greater on older islands, a pattern that is not consistent with the other genera in this radiation (Table 4.1).

The Hawaiian trigonidiines comprise the largest radiation of crickets, with species classified into three genera: *Trigonidium* (135 species), *Prolaupala* (3 species), and *Laupala* (35 species) (Figure 4.2). Scudder (1868), Brunner (1895), Perkins (1899), and Zimmerman (1948) consid-

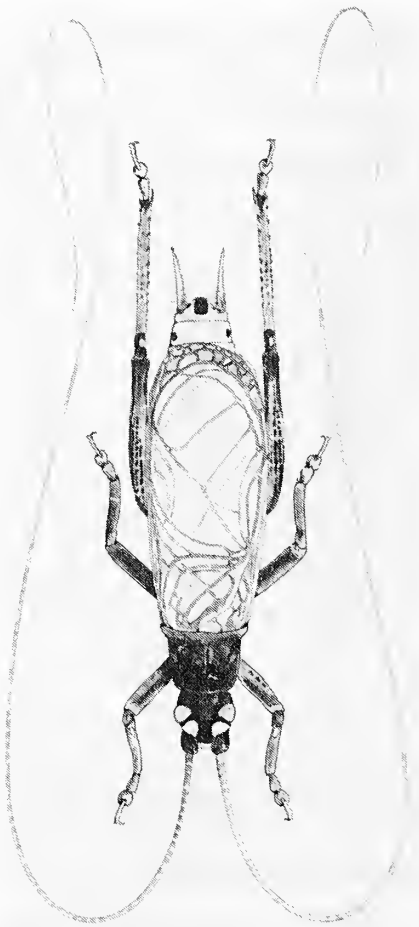


FIGURE 4.1. *Prognathogryllus robustus* (drawing by D. Otte).

ered all the native Trigonidiinae to be allied to the genus *Paratrigonidium*. In Otte (1989), Hawaiian *Trigonidium* species are referred to *Anaxipha*. Species number is roughly equal across the main islands (Table 4.1), although there is a slightly higher number of species on the middle-aged islands. The genus *Laupala* is clearly monophyletic. *Laupala* can be distinguished on the basis of the structure of the male genitalia and the female ovipositor and by increased venation in the lateral field of the tegmina (Perkins, 1899; Otte, 1994). Members of *Prolaupala* and *Lau-pala* are hypothesized to share an exclusive common ancestor (Otte, 1989, 1994; Shaw, 1993). They share common terrestrial habits and exhibit slow-pulsing, diurnal singing behavior. According to Zimmerman (1948, p. 135), "It is the chirping of these crickets that gave rise to the Hawaiian myth of the singing land snails." Whether species of *Trigonidium* are a monophyletic or paraphyletic assemblage with respect to *Prolaupala* and *Laupala* is unclear.

The predominance of single-island endemism in the native crickets suggests that inter-island migration is rare. This phenomenon, combined with the observation of extensive diversity, offers appropriate conditions in which Hawaiian geologic history may have had a significant influence on the process of diversification. Also, Otte (1989, 1994) proposed that speciation has occurred primarily within islands in the Hawaiian crickets.

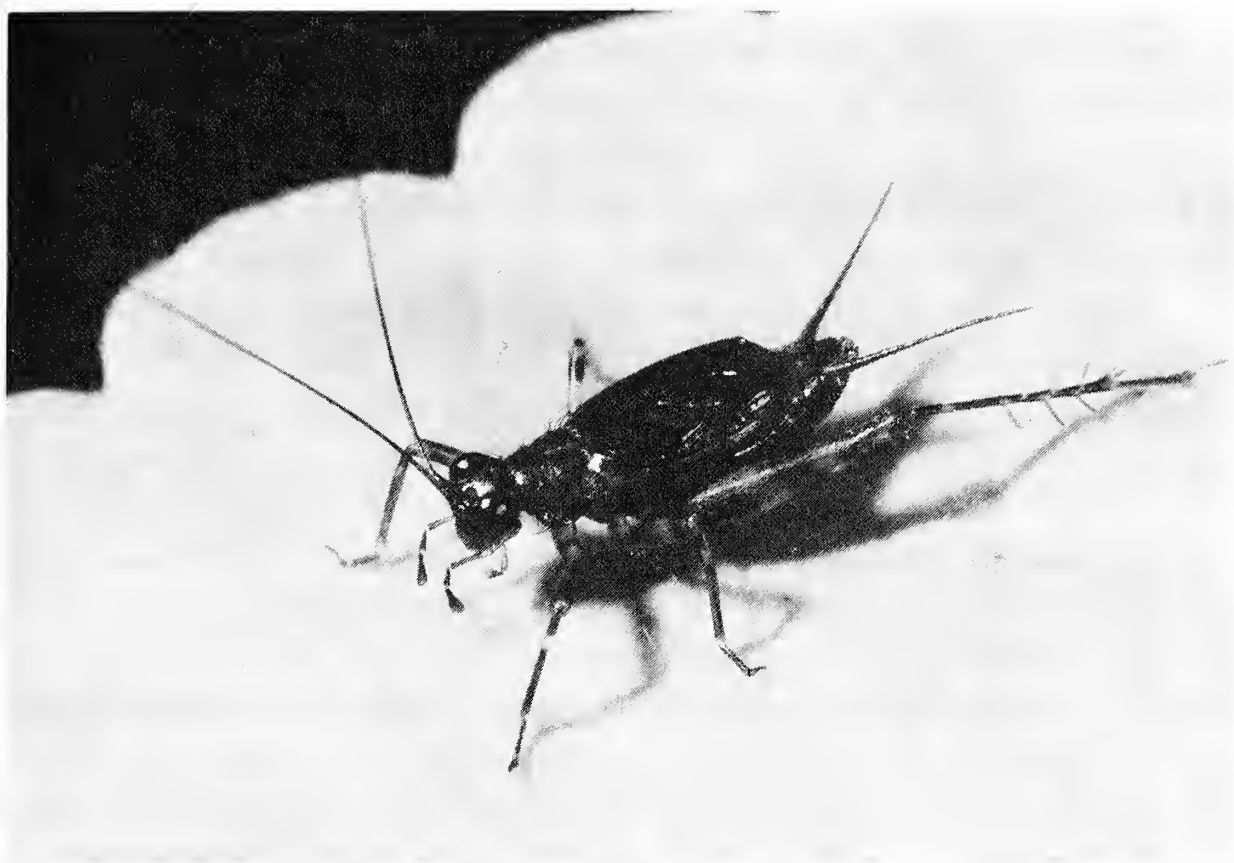


FIGURE 4.2. *Laupala paranigra* (photo by D. Funk).

This hypothesis is examined in the tree cricket genus *Prognathogryllus*, and the results are compared with the patterns found in the swordtail cricket genus *Laupala*. The distributions in both these genera are limited to the eight main islands of the Hawaiian archipelago (see Table 4.1). Otte (1989, 1994) proposed that the temporal sequence of colonization proceeded from geographically central, middle-aged islands (O'ahu or the Maui Nui complex) where the taxonomic diversity is highest to the more peripheral islands (Kaua'i and Hawai'i). In this chapter, this hypothesis is also addressed.

PHYLOGENETIC ANALYSIS IN *PROGNATHOGRYLLUS*

Cladistic analysis of the genus *Prognathogryllus* was undertaken using variation in morphological and pigmentation characters in 28 of the 36 species. These data were given in Otte (1994; reproduced in Appendixes 4.1 and 4.2), where morphological measurements derive from two individuals. In many cases, larger numbers of specimens do not exist in collections (specimens are deposited at the Philadelphia Academy of Natural Sciences). Most characters were measured on male specimens. Values for characters 11, 13, and 14 (see Appendixes 4.1 and 4.2) are missing for many taxa; excluding these characters had no effect on the

biogeographic patterns inferred from the most-parsimonious set of trees. Some species were left out of the analysis because no mature male specimens exist in collections. Species not included in the analysis are *P. haupu*, *P. wahiawa*, *P. pararobustus*, *P. giganteus*, *P. polani*, *P. olympus*, *P. makakapua*, and *P. aphrastos*.

Variation among Hawaiian cricket species is largely quantitative in nature. Differences scored distinguishing species of *Prognathogryllus* consisted of body size characters and pigmentation intensities. The character variation was coded in up to 10 states. Many characters were scored as multistate, with the assumption that these are polymorphic characters at the species level. Twenty-six characters were used in the present analysis, the number being limited by the extreme similarity among members of the genus. This type of data, in addition to temporal song characters, was used by Otte (1994) for species delimitation. Temporal song characters tend to be evolutionarily labile in crickets, particularly in the Hawaiian Islands (Otte, 1993; Shaw, 1993). Song data were therefore not considered in the present analysis. The benefits and limitations of the analysis using morphological data are discussed in more detail below.

Character distributions in *Prognathogryllus* and the nearest postulated outgroup (*Xabea* or *Neoxabea*) (Otte, 1994) provide little opportunity to polarize the phylogenetic relationships. Therefore, a phylogenetic root for *Prognathogryllus* was not estimated by outgroup comparison. Otte (1994) points out that only in the Hawaiian Islands are there tree crickets with vestigial forewings. Walker and Gurney (1967) found the characteristics of the metanotal gland to be informative in systematic research. Thus, polarity of the cladogram was estimated by considering the high position of the metanotal gland and maximum forewing length to be ancestral (characters 8 and 10, respectively; see Appendixes 4.1 and 4.2 for description of the characters and the data matrix).

Parsimony analysis was conducted with PAUP version 3.0r (Swofford, 1990b) on a Quadra Macintosh computer. Although exact parsimony algorithms are unfeasible with this many operational taxonomic units (OTUs) and the available computer power, I sampled the possible tree space by executing 1,000 replicate heuristic searches using the random addition option. All characters were designated as linearly ordered. The Lundberg rooting option in PAUP was used. The multistate characters were designated as polymorphic, as opposed to "uncertain." Coding polymorphic characters as "polymorphic at the species level," as opposed to "multistate," had some effect on the topology but not on the biogeo-

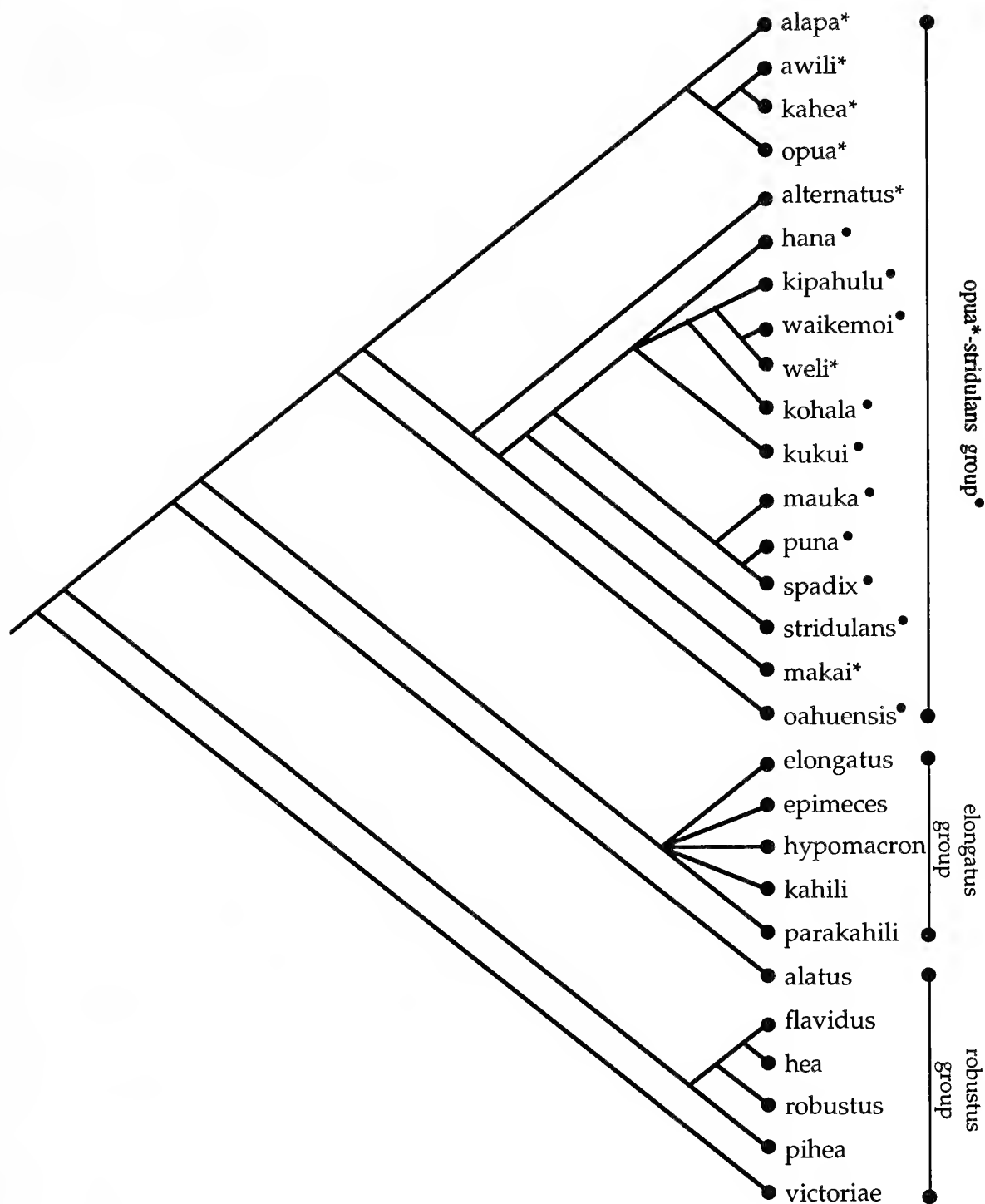


FIGURE 4.3. Strict consensus of 126 parsimony trees resulting from the maximum-parsimony analysis of the *Prognathogryllus* morphological data. Species groups are depicted to the right of the terminal taxa. An *asterisk* refers to *opua* group species; *small closed circles* refer to *stridulans* group species.

graphic implications discussed below. A strict consensus of 126 minimal length trees is shown in Figure 4.3. The consistency index (CI) is 0.531, above the 95% confidence limits for random data with an equivalent number of taxa and characters given by Klassen et al. (1991) in a recent study of CI and random data. With a retention index (RI) of 0.725, it

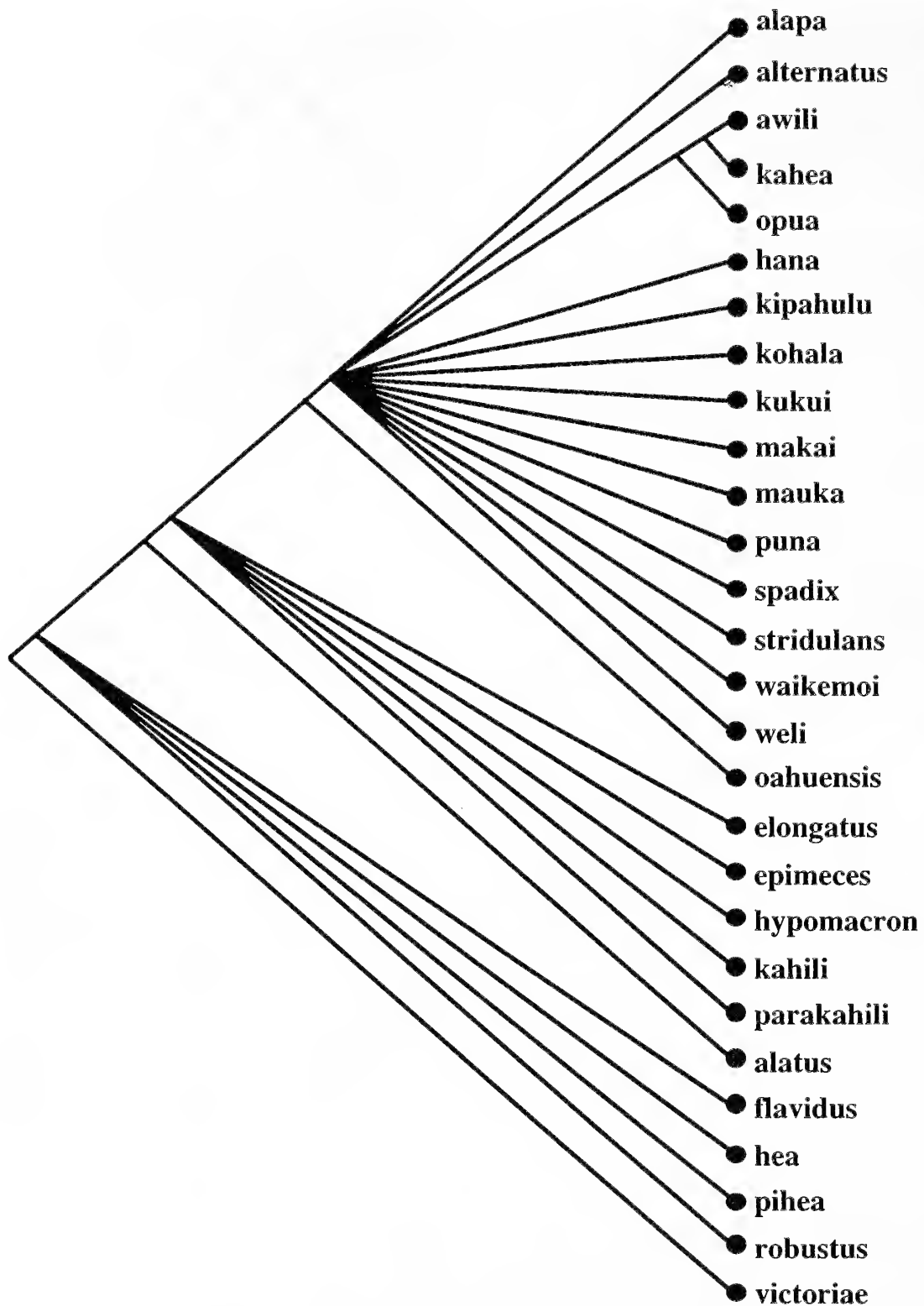


FIGURE 4.4. Strict consensus of the set of parsimonious and one-step-longer trees for *Prognathogryllus*.

seems likely that only one tree island of minimal-length trees exists (as discussed by Maddison, 1991).

The four species groups in *Prognathogryllus* designated by Otte (1994) are identified in Figure 4.3. The *robustus* group (found on Kaua'i) appears to be paraphyletic, by virtue of its basal position. However, the *elongatus* group, also found on Kaua'i, is a monophyletic group. The

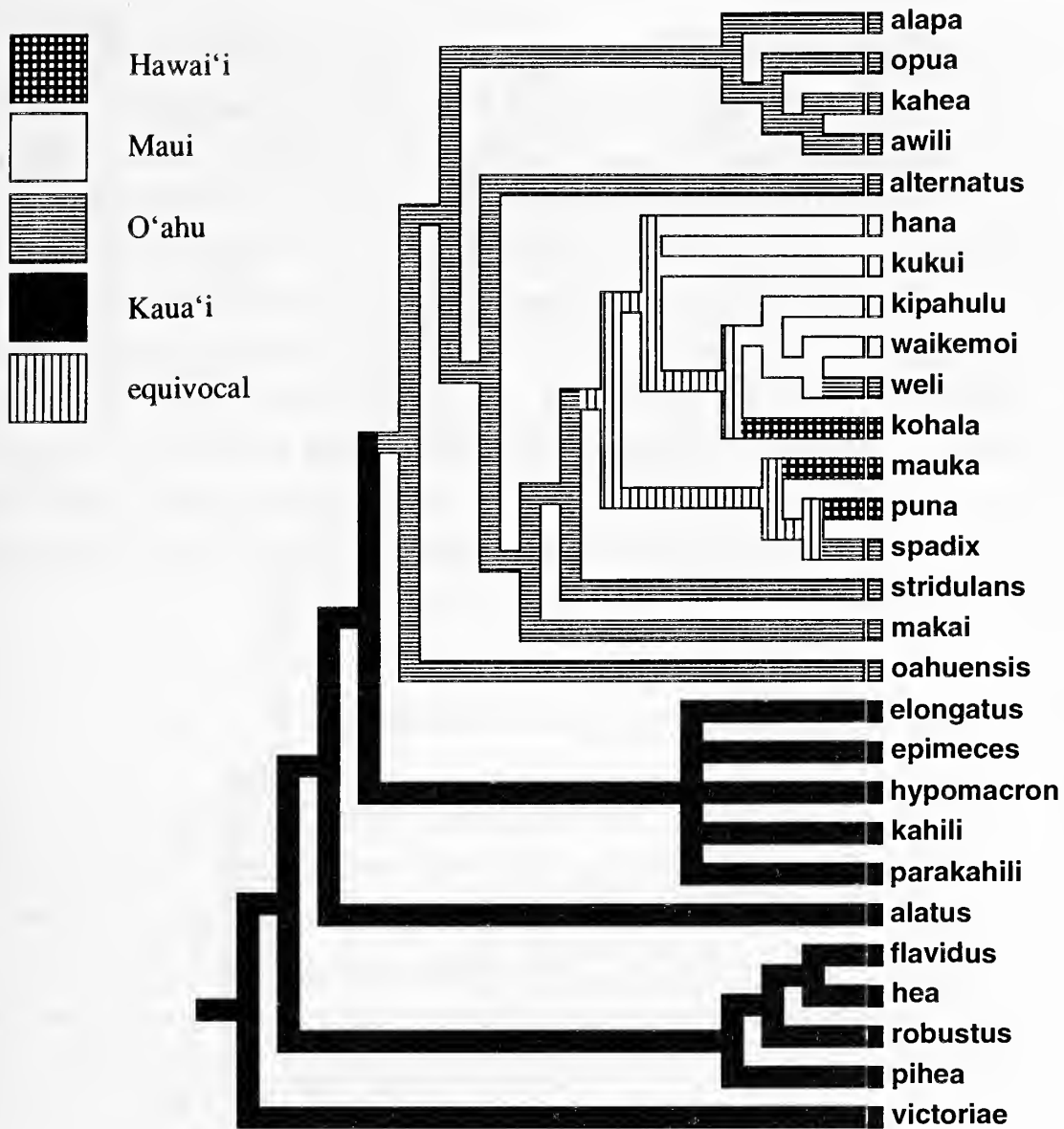


FIGURE 4.5. Historical biogeographic reconstruction in the genus *Prognathogryllus*.

opua group, from the islands of O'ahu, Maui, and Hawai'i, could not be distinguished as a distinct historical group but rather was integrated within the *stridulans* group, also represented on O'ahu, Maui, and Hawai'i. In the group of next-parsimonious trees (1,237 trees one step longer revealed by an heuristic search), the resolution degrades considerably (Figure 4.4) but primarily within the clade containing the *opua-stridulans* group. The *elongatus* group becomes paraphyletic with respect to the *opua-stridulans* clade, but all members of the *robustus* group maintain their basal position. Trees two steps longer (more than 4,400 trees) also retain these main divisions between the *robustus*, *elongatus*, and *opua-stridulans* groups.

Geographic associations of lineages and patterns of colonization were inferred using the discrete character parsimony algorithm in MacClade 3.0 (Maddison and Maddison, 1992). Island affinities of extant

species of *Prognathogryllus* and estimated geographic localities of interior nodes are presented in Figure 4.5. All Kaua'i species are found in basal positions with respect to other *Prognathogryllus* species. The extreme basal position is occupied by the Kaua'i taxon *P. victoriae* of the *robustus* group. The basal position of Kaua'i taxa is robust at least to the level of trees two steps longer. O'ahu taxa occupy the next distal positions in the phylogeny, a result that is unambiguous when considering the most-parsimonious trees and trees one step longer (see Figure 4.4). Furthermore, although comprising an unresolved polytomy, the set of most-parsimonious trees shows Maui taxa in the next more distal position (Figure 4.5). This degree of resolution is degraded when considering the group of trees one step longer (Figure 4.4).

PHYLOGENETIC ANALYSIS IN *LAUPALA*

The swordtail cricket genus *Laupala* is morphologically the most cryptic group and epitomizes Zimmerman's (1948) remark that "the Trigonidiinae is a systematically difficult assemblage." Whereas the members of other groups of native crickets may vary to some extent in body proportions, in the presence or absence of pigment patterns, file teeth number, and differences in genitalic morphology, *Laupala* species show only minor differences of a morphometric nature. Pigment differences show continuous variation from dark to less dark; genitalia differences are also quantitative in nature and are highly correlated with body size.

Systematic hypotheses were proposed by Otte (1989, 1994) based on differences in male genitalia and by Shaw (1993, in press) based on mitochondrial DNA (mtDNA) sequence variation from the 12S rRNA, 16S rRNA, and tRNA^{val} regions. The results of these studies differ significantly. The results from the molecular data are discussed here because among several analyses explored, a maximum-parsimony analysis was performed, a higher degree of systematic resolution was proposed, and polarization of the phylogeny and subsequent biogeographic inference was justified by outgroup comparison. Otte (1989, 1994) hypothesized that the origin of the current distribution of *Laupala* is concordant with the geographic center of diversity of the genus (O'ahu or Maui) and roots his phylogenetic tree based on this biogeographic proposition.

Figure 4.6 shows a strict consensus of eight equally parsimonious trees, generated through a heuristic search routine using PAUP (as above, with 1,000 random addition replications). Thirty-six unique mtDNA

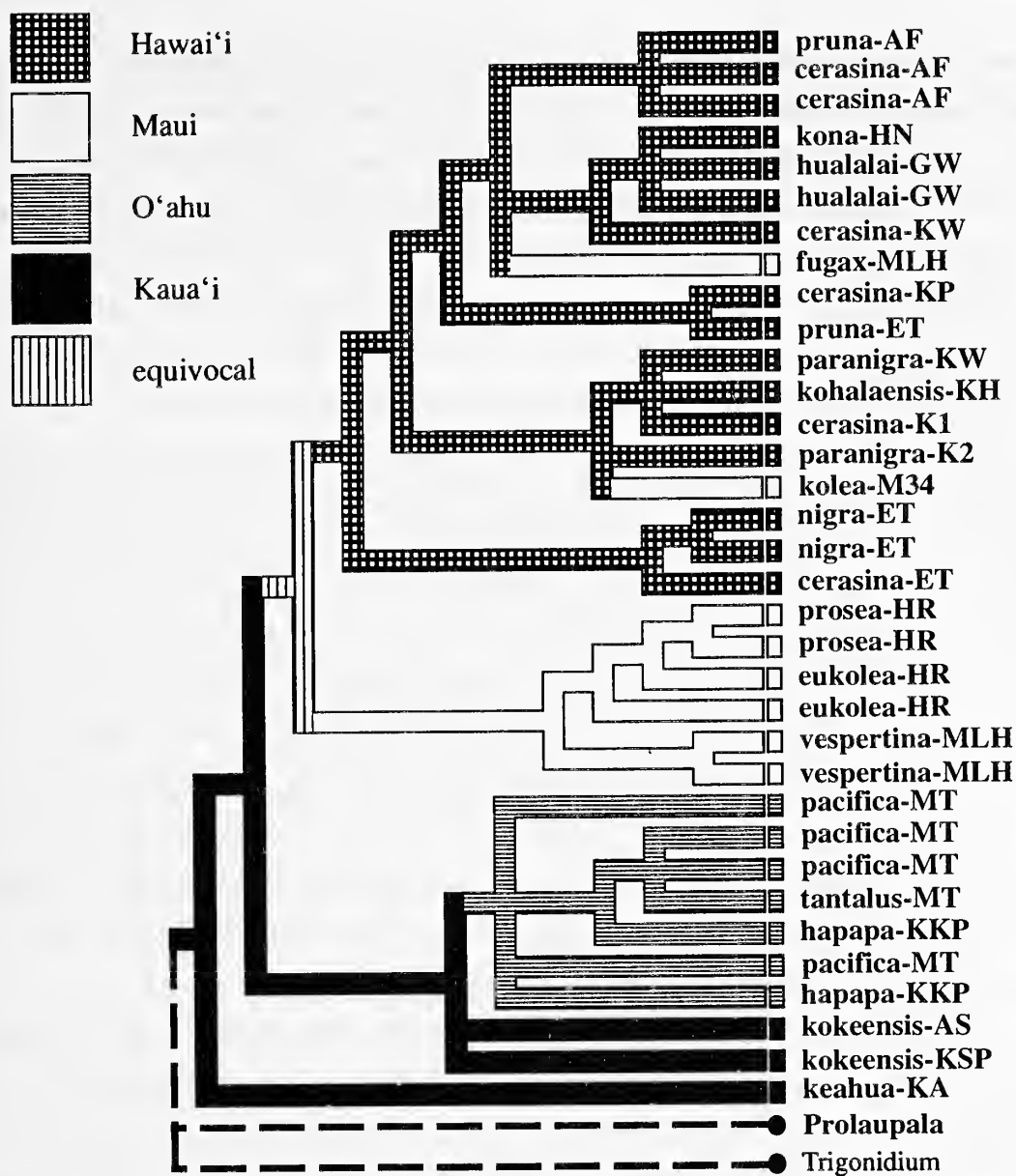


FIGURE 4.6. Historical biogeographic reconstruction in the genus *Laupala*. Terminal taxon labels indicate the species followed by the population from which a haplotype was sampled.

nucleotide sequences, sampled from 17 species of *Laupala* and 2 outgroups, were treated as the OTUs. Two Hawaiian species were included as outgroups, one from the circumglobal genus *Trigonidium* and the other from the endemic genus *Prolaupala*. A total of 74 variable characters were cladistically informative and used to estimate the topologies represented by Figure 4.6 (see Shaw, 1993, in press, for further details).

In Figure 4.6, a parsimonious reconstruction of geographic locality was superimposed using the discrete character parsimony algorithm in MacClade 3.0 (Maddison and Maddison, 1992). Only geographic data for the ingroup were used in the reconstruction. The basal position of the phylogeny is occupied by *Laupala keahua*, which occurs on Kaua'i. The next clade leads to a group of species that inhabit O'ahu, with a Kaua'i

species, *L. kokeensis*, in the basal position. As more distal positions are considered, the most-parsimonious colonization pattern remains quite simple, with the final two clades containing groups of species with distributions confined solely to the island of Maui and primarily found within the island of Hawai'i but with two back-migrations to Maui.

DISCUSSION

The most striking general pattern among the native cricket genera is single-island endemism (the only exception being *Thetella tarnis*). Perkins (1899) as well as Otte (1994) observed this phenomenon for many species. On the basis of morphology alone, one might doubt the single-island endemic status of species of *Laupala* more than species from any other endemic group. In fact, Perkins (1899) found these organisms so invariant morphologically that he designated only one species for what is now recognized by Otte (1989, 1994) as a genus of 35 species. Single-island endemism in *Laupala* is supported by the distribution of mtDNA variants across the archipelago. All sampled haplotypes were unique to single islands (Shaw, 1993, in press).

The second common feature among the generic radiations of *Laupala* and *Prognathogryllus* is that Kaua'i, the geologically oldest island supporting a large extant native cricket fauna, harbors the most basal lineages. This result was robust for trees up to two steps longer in both groups. Furthermore, in both genera, the extant taxa descended from the next more-distal lineage are found on O'ahu, the next youngest and geographically nearest to Kaua'i. For the most part, the most distal clades contain species that inhabit the islands of Maui and Hawai'i. Both generic radiations share the common feature that considerable inter-island exchange has occurred between the two youngest and geographically most proximate islands of Maui and Hawai'i. These results do not support the hypothesis of Otte (1989, 1994), who proposed that the middle-aged islands (O'ahu or possibly Maui in the case of *Laupala*), which harbor high taxonomic diversity, are the islands from which the extant radiations derived. Under Otte's hypothesis, one would expect that species in the most basal positions would occur on O'ahu or Maui.

A third common feature of the *Laupala* and *Prognathogryllus* radiations is that many species do find their closest relatives within the same island. Otte (1989) had hypothesized previously that most speciation in Hawaiian crickets occurs within islands, as opposed to the predominant

inter-island mode of speciation in the picture-winged Hawaiian *Drosophila* (Carson and Kaneshiro, 1976). Diversity in the two cricket genera studied here appears to have occurred via colonization to new islands as they arose in geologic time but less frequently than in Hawaiian *Drosophila*.

Evidence for paleogeographic patterns in the relationships of native crickets is exciting for several reasons. First, the colonization patterns in Figures 4.5 and 4.6 raise the possibility that the origins of both the oecanthine and trigonidiine radiations may predate their current geographic circumstances in the Hawaiian Islands. The oecanthine radiation offers a compelling geographic distribution, which may provide further insight. The sister group of *Prognathogryllus*, comprising the endemic genera *Leptogryllus* and *Thaumtogryllus*, has a representative on Nihoa, a geologic relict of the high-island part of the chain (Stearns, 1985; Carson and Clague, this volume, Chapter 2). If *T. conanti* (the Nihoa species) is a biogeographic relict of a past oecanthine fauna on Nihoa, it should reside in a basal phylogenetic position with respect to the *Thaumtogryllus* clade. A past oecanthine fauna on Nihoa would also suggest that the fauna on younger islands is derived and therefore that *Prognathogryllus* is a monophyletic sister group to *Leptogryllus* and *Thaumtogryllus*, providing evidence against a paraphyletic relationship. Furthermore, through phylogenetic investigation one might expect a similar older-to-younger island correspondence of basal and distal phylogenetic positions in the *Leptogryllus* and *Thaumtogryllus* radiations. Likewise, if the swordtail crickets are derived from a past fauna on islands older than the current high islands, *Trigonidium* species from Kaua'i should occur in basal phylogenetic positions as discussed here for the *Laupala* radiation.

Second, a geochronological influence is important because it creates the opportunity to investigate repeated patterns in history. Infrequent colonizations of new islands, followed by adaptive intra-island radiations and speciation, may offer circumstances in which similar evolutionary trends occur in parallel. A phylogenetic pattern with considerable inter-island resolution provides a context for focusing on shifts of reproductive and ecological suites of characters. The relative evolutionary rate of these shifts implicates the importance of different selective pressures in the diversification process.

In *Laupala*, similar trends have already become clear. On any given island, one may find anywhere from one to four sympatric species present, where species are distinguishable by different songs (e.g., a slow, a

medium, and a fast singer). Convergent patterns in the temporal structure of the calling song and the communities that they comprise occur within three of the high islands (O'ahu, Maui, and Hawai'i) (Shaw, 1993). Ecological differences between species are subtle. Although *Laupala* species probably depend on certain elements of forest structure (e.g., sufficient understory or leaf litter), they can survive independently of native plants. *Laupala* species move into non-native forests such as guava or eucalyptus and thrive in the laboratory on a diet of standard Purina cricket chow. To what extent ecological boundaries exist among these sympatric species of *Laupala* is not clear.

In contrast to species of *Laupala*, which occur in sympatric communities apparently without host plant dependency, species in *Prognathogryllus* form identifiable ecological groups and occur in association with a variety of native plants, such as *Metrosideros polymorpha* Gaud. (Myrtaceae) and *Freycinetia arborea* Gaud. (Pandanaaceae). The most closely related species of *Prognathogryllus* occur in disjunct ranges. Sympatric associations are concomitant with more distinct differences in host association and greater phylogenetic diversity and, thus, greater island age (e.g., members of the *robustus* and *elongatus* groups on Kaua'i). *Prognathogryllus robustus* has been found exclusively in association with 'ohi'a (*Metrosideros polymorpha*), where the purple or reddish individuals are cryptic against the red leaflets and small branches of 'ohi'a trees. At night, males and females are often among the flowers in the terminal portions of the trees. *Prognathogryllus robustus* possesses cryptic coloration against the background of 'ohi'a blossoms and foliage. Other members of the *robustus* group have similar stout body proportions but differ to the largest degree in pigmentation patterns. Members of the *elongatus* group, although only found in native forest, do not appear to be confined to any one particular native plant. They also cavort high in treetops at night but apparently pass the daylight hours closer to the ground in hollowed twigs or dried fern fronds. By contrast, members of the *elongatus* group are largely indistinguishable morphologically but have distinctive songs. Thus within *Prognathogryllus*, prominent patterns of diversity are apparent both in ecological and reproductive characters.

The characters that make up the data set for *Prognathogryllus* are those used in the species-level taxonomy of the group. The benefits of this analysis are that it serves to establish explicitly hypotheses, which have previously only been suggested, and it allows the exploration of the phylogenetic information in species-level characters. A similar data set for *Laupala* proved uninformative. In *Prognathogryllus*, although some his-

torical information apparently exists in these characters, they are less than ideal for several reasons. As mentioned above, the variation among species is quantitative, and thus a discrete coding system was chosen so that maximum-parsimony analysis could be performed. In cladistic analyses, discrete characters with nonarbitrary categories are preferred (like the molecular characters used in the analysis of *Laupala*), but these kinds of data are currently unavailable for *Prognathogryllus*.

The conclusions reached in the analysis of the *Prognathogryllus* data set are dependent on the quality of the phylogenetic inference, and there are several weaknesses in the present analysis. Partly due to the quantitative nature and arbitrary divisions imposed, polymorphisms had to be dealt with in the analysis of *Prognathogryllus*. Also, the characters that define different morphological groups in this genus, which often correspond to taxonomic species, are variable, and the distribution of variation in nature overlaps to some extent. To what extent they are variable and to what extent natural gaps might exist in the distributions of these characters across the genus can only be ascertained through more extensive population sampling. I chose to represent species as polymorphic, as opposed to deciding on a single character value for each species based on one of the available methods for continuous character coding (e.g., methods discussed by Archie, 1985). The strategy in this analysis was chosen primarily because of the limited population sample size for each species. Recoding of polymorphisms at the species level had no effect on the outcome of the biogeographic conclusions, although the topology was affected in minor ways. This alternative approach codes the species as polymorphic rather than allowing the maximum-parsimony algorithm to assign a monomorphic ancestral state as PAUP does under a polymorphic multistate designation (see Maddison and Maddison, 1992, for a useful discussion of polymorphisms).

The Hawaiian tree crickets, as well as the swordtail crickets, have diverged from their original founder lineages to such a degree that they were taxonomically misplaced by Perkins (1899) and Zimmerman (1948). The close relationship among species within the endemic genera further clouds estimating a root for the cladogram with morphological data. Thus, another weakness of the *Prognathogryllus* analysis is that the polarity of the cladogram is inferred on the basis of two characters (although a midpoint root did not change the biogeographic pattern inferred). A preferred outgroup comparison approach, such as that taken in the *Laupala* analysis, might be feasible if molecular data were available.

ACKNOWLEDGMENTS

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APPENDIX 4.1. Character List for *Prognathogryllus*

1. Face, color of frons: 0 = pale; 1 = variegated pale and brown; 2 = brown; 3 = dark brown to black.
2. Head, color of rostrum: 0 = pale; 1 = brown; 2 = dark brown or black.
3. Dorsum of head, color of area medial to eyes: 0 = pale; 1 = brown; 2 = dark; 3 = all black.
4. Head, occipital stripes: 0 = absent; 1 = faint; 2 = present.
5. Pronotal length/greatest pronotal width: 0 = 0.80–0.84; 1 = 0.85–0.89; 2 = 0.90–0.94; 3 = 0.95–0.99; 4 = 1.00–1.04; 5 = 1.05–1.09; 6 = 1.10–1.14; 7 = 1.15–1.19; 8 = 1.20–1.24.
6. Pronotum, color of dorsal surface: 0 = mostly pale; 1 = slightly variegated; 2 = highly variegated; 3 = mostly dark but with pale marks; 4 = all black.
7. Pronotum, lateral lobe color: 0 = pale or brown; 1 = dark above, pale below; 2 = all dark brown or black.
8. Metanotal gland, position of orifice: 0 = low; 1 = moderately high; 2 = high.
9. Number of file teeth: 0 = 50–99; 1 = 100–149; 2 = 150–199; 3 = 200–249; 4 = 250–299; 5 = 300–349; 6 = 350–399; 7 = >400.
10. Male forewing length/pronotal length: 1 = 2.0–2.4; 2 = 2.5–2.9; 3 = 3.0–3.4; 4 = 3.5–3.9; 5 = 4.0–4.4; 6 = 4.5–4.9; 7 = 5.0–5.4.
11. Female forewing length/pronotal length: 1 = 0.55–0.99; 2 = 1.00–1.49; 3 = 1.50–1.99; 4 = 2.00–2.49; 5 = 2.50–2.99; 6 = 3.00–3.49.
12. Male mirror length/mirror width: 0 = 1.00–1.09; 1 = 1.10–1.19; 2 = 1.20–1.29; 3 = 1.30–1.39; 4 = 1.40–1.49; 5 = 1.50–1.59; 6 = 1.60–1.69; 7 = 1.70–1.79; 8 = 1.80–1.89; 9 = 1.91–1.99.
13. Female cercal length/femur III length: 1 = 0.50–0.59; 2 = 0.60–0.69; 3 = 0.70–0.79; 4 = 0.80–0.89; 5 = 0.90–0.99; 6 = 1.00–1.09; 7 = 1.10–1.19.
14. Female ovipositor length/femur III length: 0 = 0.50–0.59; 1 = 0.60–0.69; 2 = 0.70–0.79; 3 = 0.80–0.89; 4 = 0.90–0.99; 5 = 1.00–1.09; 6 = 1.10–1.19; 7 = 1.20–1.29; 8 = 1.30–1.39; 9 = 1.40–1.49.

15. Abdomen dorsum, last segments: 0 = pale; 1 = spotted; 2 = black.
16. Epiproct, central area: 0 = pale; 1 = black.
17. Subgenital plate color: 0 = pale; 1 = with small dark spots; 2 = dark brown or black.
18. Front and middle femora color: 0 = mostly pale; 1 = mostly dark.
19. Tibiae: 0 = without dark ring near knee; 1 = with dark ring near knee.
20. Hind femur color: 0 = mostly pale brown or tan; 1 = pale to dark; 2 = black.
21. Hind femur, patterning on outer face: 0 = absent; 1 = faint; 2 = distinct; 3 = all black.
22. Femora III, knees: 0 = pale; 1 = dark.
23. Male tibiae III length/femur III length: 0 = 0.30–0.39; 1 = 0.40–0.49; 2 = 0.50–0.59; 3 = 0.60–0.69; 4 = 0.70–0.79; 5 = 0.80–0.89; 6 = 0.90–0.99; 7 = 1.00–1.09; 8 = 1.10–1.19; 9 = 1.20–1.29.
24. Hind femur length: 0 = 6–7 mm; 1 = 7–8 mm; 2 = 8–9 mm; 3 = 9–10 mm; 4 = 10–11 mm; 5 = 11–12 mm; 6 = 12–13 mm; 7 = 13–14 mm; 8 = 14–15 mm; 9 = 15–16 mm.
25. Number of inner spines on tibiae III: 0 = 5–9; 1 = 10–14; 2 = 15–19; 3 = 20–24; 4 = 25–29; 5 = 30–34; 6 = 35–39; 7 = 40–44.
26. Number of middle spines on tibiae III: 0 = 0–9; 1 = 10–14; 2 = 15–19; 3 = 20–24; 4 = 25–29; 5 = 30–34.
27. Number of outer spines on tibiae III: 0 = 10–14; 1 = 15–19; 2 = 20–24; 3 = 25–29; 4 = 30–34; 5 = 35–39.

APPENDIX 4.2. Data Matrix of Character States for the Genus *Prognathogryllus*

The characters and character states are defined in Appendix 4.1. Character states separated by a slash indicate polymorphism.

| | | Character | | | | | | | | | | | | | | | | | | | | | | | | | | |
|----------------------|-----|-----------|-----|---|-----|-----|-----|---|-----|-----|-----|-----|-----|-----|----|----|----|----|----|----|-----|----|-----|-----|-----|-----|-----|--|
| Species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | |
| <u>P. alapa</u> | 1 | 2 | ? | | 0 | 1 | 0 | 2 | 0 | 3 | 2 | 2 | 3 | 3 | 2 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 6 | 0 | 1 | 1 | |
| <u>P. alatus</u> | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 5 | 1 | 2 | 3 | 9 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 4 | 1 | ? | 1 | |
| <u>P. alternatus</u> | 2 | 1 | 1 | 0 | 0/2 | 2 | 0 | ? | 0 | 4/5 | 2 | 1/2 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | ? | 0/1 | 3/6 | 1/2 | 0/2 | 1/2 | |
| <u>P. awili</u> | 3 | 2 | 2 | 0 | 0/3 | 3/4 | 2 | 2 | 0/1 | 3 | ? | 3 | ? | ? | 2 | 1 | 2 | 1 | 0 | 2 | 3 | 1 | 1 | 3/5 | 1 | 2 | 2 | |
| <u>P. elongatus</u> | 0 | 0 | 0 | 0 | 4/8 | 0 | 0 | 0 | 0 | 1/3 | 2/3 | 5/8 | 3/4 | 0/2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6/9 | 3/4 | 2/3 | 0 | 2/3 | |
| <u>P. epimeces</u> | 0 | 0 | 0 | 0 | 5/6 | 0 | 0 | 0 | 0 | 2 | 3 | 6 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 4/5 | 2/3 | 0 | 2/3 | |
| <u>P. flavidus</u> | 0/3 | 0/2 | 0/2 | 0 | 0/3 | 0/4 | 0/2 | 0 | 2 | 4/5 | ? | 0/2 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0/1 | 0 | 6/7 | 3/4 | 1/2 | 0 | 0/1 | |
| <u>P. hana</u> | 3 | 2 | 2 | 1 | 1/6 | 1 | 0 | 2 | 1 | 2/3 | 2/3 | 2/5 | 1/3 | 0/1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 4/5 | 2/3 | 0/3 | 2/4 | |
| <u>P. hea</u> | 3 | 2 | 2 | 0 | 0 | 4 | 2 | 2 | 2 | 5 | ? | 0 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 2 | ? | ? | ? | |
| <u>P. hypomacron</u> | 0 | 0 | 0 | 0 | 1/3 | 0 | 0 | 0 | 0 | 2 | ? | 6/8 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7/8 | 3 | 2/3 | 0 | 0/3 | |
| <u>P. kahea</u> | 3 | 2 | 2 | 0 | 1/2 | 2/3 | 2 | 2 | 1 | 3/4 | 2 | 2/3 | 6 | 7 | 2 | 1 | 2 | 0 | 1 | 1 | 2 | 1 | 0/1 | 3/5 | 1 | 0/1 | 1/2 | |
| <u>P. kahili</u> | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 2 | ? | ? | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 4 | 2 | 1 | 2 | |
| <u>P. kipahulu</u> | 3 | 2 | 2 | 2 | 3 | 1 | 0 | 1 | 4 | 3 | ? | 4 | ? | ? | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 5 | 3 | 1 | 2 | |
| <u>P. kohala</u> | 3 | 2 | 2 | 2 | 1/2 | 1 | 0 | 1 | 2 | 3 | ? | 3/4 | ? | ? | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 2 | 0 | 2 | |
| <u>P. kukui</u> | 3 | 2 | 2 | 0 | 2 | 1 | 0 | 1 | 1 | 3 | 2 | 1/4 | 1/2 | 0/1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 3/4 | 2 | 0/2 | 1/3 | |
| <u>P. makai</u> | 1 | 2 | 0 | 0 | 0/2 | 1 | 0 | 2 | 0 | 3/4 | 2 | 1/4 | 2/3 | 0/1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0/1 | 2/4 | 1/2 | 1/3 | 2/3 | |
| <u>P. mauka</u> | 3 | 2 | 2 | 0 | 1/3 | 0 | 0 | 2 | 4/5 | 3/4 | ? | 1/3 | ? | ? | ? | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 3/4 | 1/2 | 1/2 | 2/4 | |
| <u>P. oahuensis</u> | 0 | 0 | 2 | 0 | 2/6 | 1 | 0 | 2 | 0 | 2/4 | 2 | 4/7 | 3 | 4 | 1 | 1 | 1 | 0 | 0 | 0 | 0/1 | 0 | 1/3 | 3/4 | 1/3 | 0/2 | 0/3 | |
| <u>P. opua</u> | 3 | 2 | 1 | 0 | 1/2 | 2 | 1 | ? | 0 | 2/3 | 3 | 1/3 | 4 | 4 | 2 | 1 | 2 | 0 | 0 | 0 | 1/2 | 0 | 0/1 | 6/8 | 0/1 | 0/2 | 1/2 | |
| <u>P. parakahili</u> | 0 | 0 | 0 | 0 | 6/7 | 0 | 0 | 0 | 0 | 2 | 3 | 4/6 | 3 | 1/2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6/7 | 5 | 2/3 | 0/1 | 2/3 | |
| <u>P. pihea</u> | 2 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 1 | 5 | ? | 0 | ? | ? | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 7 | 2 | 1 | 0 | 0 | |
| <u>P. puna</u> | 3 | 2 | 2 | 0 | 3 | 0 | 0 | 2 | ? | 3 | ? | 7 | ? | ? | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 3 | 1 | 0 | 2 | |
| <u>P. robustus</u> | 3 | 2 | 2 | 2 | 0 | 2 | 2 | 0 | 1 | 4/6 | 4/6 | 0/1 | 3/4 | 3/5 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 7/8 | 1/3 | 1/2 | 0 | 0/1 | |
| <u>P. spadix</u> | 3 | 2 | 2 | 0 | 2/4 | 0 | 0 | 2 | 0 | 2/3 | 2 | 4/5 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1/2 | 1/5 | 2 | 0/1 | 1/2 | |
| <u>P. stridulans</u> | 1 | 1 | 2 | 0 | 2/6 | 2 | 0 | 2 | 1 | 2/3 | 2 | 3/6 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 4/5 | 2/4 | 0/2 | 2/4 | |
| <u>P. victoriae</u> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 5 | ? | 0 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 2 | 2 | 0 | 1 | |
| <u>P. waikemoi</u> | 3 | 2 | 2 | 2 | 1 | 1 | 0 | 1 | 7 | 4 | ? | 2 | ? | ? | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 5 | 1 | 2 | 4 | |
| <u>P. weli</u> | ? | ? | ? | 2 | 0 | 1 | 0 | 1 | 0 | 3 | ? | 2 | ? | ? | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 7 | 1 | 2 | 2 | |

5

Chromosomes and Male Genitalia of Hawaiian *Drosophila*

Tools for Interpreting Phylogeny and Geography

KENNETH Y. KANESHIRO,
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Nearly 35 years ago, Zimmerman (1958) put out a challenge to geneticists and evolutionists to investigate what he considered to be an “extraordinary” fauna of Drosophilidae. He surmised that “It is possible that the Hawaiian drosophilid fauna may be the most remarkable in the world.” He was amazed that “there may be as many as 300 species concentrated in an area smaller than the little state of Massachusetts. . . .” For three decades now (since the summer of 1962), a team of more than 75 evolutionary biologists from nearly every aspect of biology has studied this amazing group of insects, and as such, the taxonomic treatment of the endemic Hawaiian species in this family of flies has been supplemented by studies of morphology, genetics, geographic distribution, ecology, behavior, developmental biology, cytology, population biology, biochemistry, and molecular biology.

In *Island Populations*, Williamson (1981, p. 168) described the multidisciplinary approach to the study of the Hawaiian Drosophilidae as being one of the most outstanding in evolutionary biology. He stated:

Of all the groups of organisms, plants or animals, that can be studied on islands, the Hawaiian Drosophilidae are supreme. This is why. There are a great many species; their ecology is very varied; and, most important, a genetic analysis is possible. In other groups of organisms, it is possible to study allozyme frequencies, metaphase chromosomes and so on. So far though, only in the Drosophilidae can we study evolution on an archipelago of a group with polytene chromosomes. These giant chromosomes,

found in the salivary glands and other parts of the fly larvae, show complex sequences of bands down their length whose patterns differ in different species. This variation in banding produces detailed and sound evidence of phylogenetic history. In the Hawaiian *Drosophilidae*, this allows us to postulate at which points in evolutionary history the stock has immigrated to a different island and at what point it has evolved on one island.

In this chapter, we discuss the significance of a comparative study of the banding patterns of the giant polytene chromosomes for interpreting phylogenetic relationships among related species. When superimposed on the biogeographic distribution of the species and a comparative study of the structures of the male genitalia, the chromosomal phylogeny sets the foundation on which other sophisticated tools of evolutionary biology such as the DNA sequencing techniques can be applied to further our understanding of the evolutionary history of this remarkable group.

THE GEOLOGY OF THE HAWAIIAN ISLANDS

A key feature of the evolutionary biology of endemic fauna and flora of the Hawaiian Islands is the sequential formation of each of the high islands as the Pacific tectonic plate moved over a fixed hot spot beneath the large Pacific plate (Clague and Dalrymple, 1987; see also Carson and Clague, this volume, Chapter 2). Thus, approximately 5 million years ago (Ma), Kaua'i, the oldest of the present high islands, was in the position where the island of Hawai'i is currently situated. As the plate moved in a northwesterly direction at a rate of about 9 cm/year, the island of O'ahu emerged approximately 3.7 Ma, followed by the Maui Nui complex of islands (Moloka'i, Kaho'olawe, Lana'i, and Maui) 0.75 to 1.9 Ma. Hawai'i, the youngest of the present high islands, which is currently situated over the hot spot and which continues to have major volcanic activity, began to form less than 0.5 Ma.

Thus, evolutionary biologists are presented with a linear sequence of high islands and their constituent volcanoes, each formed in chronological sequence, with Kaua'i currently the oldest and Hawai'i the youngest. In most cases, it turns out that the most ancestral species of a group of related species is found on Kaua'i and that the most derived species is found on the island of Hawai'i. Therefore, it is possible to trace the evolutionary sequence of species formation with corroborative evidence from the geologic history of the Hawaiian Islands, which can serve as an

important tool for increasing our understanding of the phylogenetic relationships among related taxa.

TAXONOMIC STATUS OF THE HAWAIIAN DROSOPHILIDAE

Currently, 511 species (Hardy and Kaneshiro, 1981) have been named and described in the family Drosophilidae from the Hawaiian archipelago. Another 250 to 300 undescribed species have been collected. As new localities are sampled, new species continue to be discovered, and estimates of 1,000 species in this fauna have been proposed (Kaneshiro, 1993). About 20 additional species, mostly widespread associates of humans, have been introduced into the islands in historic times.

Originally, the endemic Drosophilidae were described in nine genera (Hardy, 1965), but several lines of evidence indicate that all species are part of only two lineages, *Drosophila* and *Scaptomyza* (Throckmorton, 1966; Kaneshiro, 1976). On the basis of a comparative study of the internal anatomy, Throckmorton (1966) observed that although the Hawaiian species could be divided into two main groups, they showed distinct similarities, which suggested that the entire group may have arisen from a single introduction. He stated that "Hawai'i must be considered to be the only place in the world where the otherwise sharp distinctions between *Scaptomyza* and *Drosophila* tend to disappear." However, molecular studies of a larval protein (Beverley and Wilson, 1984) and recent DNA sequences of the alcohol dehydrogenase locus (Thomas and Hunt, 1991) suggest that the separation of scaptomyzoid and drosophiloid lineages took place at least 24 Ma. In view of the evidence that there were once high islands well to the northwest of Kaua'i (see Carson and Clague, this volume, Chapter 2), divergence between the two lineages could either have occurred on older islands or may be the result of two independent introductions from continental ancestors. Thus, despite extreme morphological diversity, which led earlier taxonomists to divide the group into nine genera, the endemic Hawaiian drosophilids appear to be very closely related phylogenetically. Comparative studies of the DNA (see review in DeSalle and Hunt, 1987) also appear to corroborate Throckmorton's conclusions.

Kaneshiro (1976), by pooling corroborating observations from studies of the internal anatomy (Throckmorton, 1966), mating behavior (Spieth, 1966, 1968), ecology (Heed, 1968, 1971), cytology (Stalker,

1970, 1972; Yoon et al., 1972), and especially a comparative study of the external male genitalia (Kaneshiro, 1976), presented evidence for the existence of only two major lineages (genera) in the evolution of the Hawaiian Drosophilidae, *Scaptomyza* and *Drosophila*. It was demonstrated that the "key" characters previously used to differentiate the drosophilid species into more than two generic groupings were not "good" generic characters and that most of these variations in external morphology were phylogenetically superficial.

Species in the genus *Drosophila* have been separated into species groups based primarily on external morphological characteristics of males (i.e., secondary sexual characters) (Hardy and Kaneshiro, 1981). These informal groupings of species have been designated primarily to facilitate discussions about species with synapomorphic characteristics, although these are not necessarily relevant for subgeneric classification. For example, about 100 species exhibit moderate to extreme modifications on the labellum of the mouthparts and have been grouped into the "modified mouthparts" species group. This large and heterogeneous group, however, is likely to be composed of many species complexes. Similarly, the "modified tarsus" species group can be further subdivided into the "split tarsus," "spoon tarsus," and "bristle tarsus" subgroups.

THE PICTURE-WINGED SPECIES GROUP

The "picture-winged" group of Hawaiian *Drosophila*, comprising 111 species, has attracted the most research attention. Most picture-winged species are large-bodied with striking maculations on the wings that vary from species to species. Many of these species can be reared in the laboratory, and detailed analyses of their morphology, behavior, genetics, cytology, proteins, and DNA can be conducted. These species provide extremely favorable cytological material and are particularly good subjects for comparisons of the banding sequences of the polytene chromosomes. Carson and his collaborators conducted an extensive study (see reviews in Carson, 1987b, 1992b) of the inversion patterns of the giant polytene chromosomes of 106 picture-winged species, and they developed a pattern of relationships based on the presence or absence of inversions relative to an arbitrary standard. Kaneshiro (1969) studied the male genitalic structures of this group and found that similarities in the shape of the phallic organs, especially that of the penis, are useful for separating the picture-winged species into species subgroups and com-

plexes. For the most part, the relationships based on male genitalia complemented those of the chromosomal characters.

We use examples from the picture-winged species group to illustrate the value of analyses of chromosomal inversion patterns together with a comparative study of conservative morphological characters, such as the male genitalia, for interpreting their phylogenetic relationships.

CHROMOSOMAL TRACERS OF PHYLOGENY

A main attribute of many dipteran groups, including that of *Drosophila*, is the giant polytene chromosomes found in the cells of the salivary glands of the mature larvae. The banding patterns observed in the salivary gland chromosomes offer an abundance of details that can be used for comparative studies of gene order within and between species. Chromosomal rearrangements, primarily a result of paracentric inversions, can be used to trace the evolutionary history of groups of closely related species that are similar in banding sequences. The original unrooted chromosomal phylogeny of the picture-winged species group (Carson, 1992b) assumed that paracentric inversions with two-break rearrangements are unique events, and species carrying this same arrangement in their chromosomes were presumed to have been derived from a common ancestor. More complex rearrangements with either overlapping inversions or inversions occurring within previously inverted sections with multiple breaks were assumed to reflect a step-wise evolution in the chromosomes. In most cases, a phylogenetic sequence of species formation can be traced by deciphering the sequence of step-wise rearrangements in the six polytene chromosomes, five long and one short. Each species was differentiated by a formula describing the number and position of inverted segments relative to the arbitrarily chosen *D. grimshawi* standard.

PHYLOGENETIC ANALYSIS OF CHROMOSOMAL DATA

Carson's (1992b) data from 106 species of picture-winged *Drosophila* were coded for chromosomes X, 2, 3, 4, and 5, according to whether an inversion sequence was absent (0), present and fixed (1), or polymorphic (0,1). Characters were analyzed using PAUP (Swofford, 1991), and character states were polarized as primitive or derived by outgroup comparison (Maddison et al., 1984). Heuristic searches were conducted to find the shortest trees. The data were then reanalyzed by successive approxi-

mations, weighting characters according to their rescaled consistency index (RC) (Farris, 1969, 1989).

Drosophila primaeva from the island of Kaua'i was chosen as an outgroup for the 106 species of picture-winged *Drosophila*. Although *D. primaeva* and its sympatric close relative, *D. attigua*, are not "true" picture-winged species in that they lack distinct maculations on the wings, their chromosomal banding sequences can be completely resolved in terms of the *D. grimshawi* standard. In *D. primaeva*, a sequence of bands on chromosome 5 has a gene order identical to the homologous sequence found on the same chromosome in *D. colorata*, a species from Japan (Stalker, 1972). The latter is now considered to be a member of the *D. melanica* group (Beppu, 1988), which is widespread on both the Asian and North American continents. Because all other picture-winged species of Hawai'i have this sequence broken up by inversions, *D. primaeva* is clearly the Hawaiian species most closely related to continental species. This provides strong evidence that the "direction of evolution" has been from a continental species, through *D. primaeva* to the other picture-winged species of Kaua'i and the newer Hawaiian Islands. Geologic considerations would seem to exclude the reverse order of evolution. For further discussion, see Carson and Yoon (1982).

To establish the basic structure of the tree, we used 30 taxa that represented most chromosomal types. The taxa used were *Drosophila attigua*, *D. bostrycha*, *D. clavisetae*, *D. crucigera*, *D. discreta*, *D. distinguenda*, *D. engyochracea*, *D. fasciculisetae*, *D. flexipes*, *D. gradata*, *D. grimshawi*, *D. hawaiiensis*, *D. heteroneura*, *D. melanocephala*, *D. neopicta*, *D. nigribasis*, *D. oahuensis*, *D. obscuripes*, *D. ochracea*, *D. ornata*, *D. orphnopeza*, *D. pilimana*, *D. primaeva*, *D. psilotarsalis*, *D. punalua*, *D. setosifrons*, *D. setosimentum*, *D. spaniothrix*, *D. truncipenna*, and *D. virgulata*. A heuristic search generated 24 trees, length 147, which were then weighted according to the RC and reanalyzed, resulting in the same 24 trees, with a consistency index (CI) of 0.998 and a retention index (RI) of 0.998. Strict consensus of these trees divided the taxa into three major clades and the *D. primaeva*-*D. attigua* sibling species pair. The first clade to branch off is the *adiastola* clade, which is defined by six nonhomoplasious characters (2d, 3k, 4o, Xu, Xx, and Xy). The second to branch off is the *planitibia* clade, which is defined by two nonhomoplasious characters (3d, Xj). The final group, the *grimshawi* clade, is characterized by three nonhomoplasious characters, the standard sequences corresponding to Xi, Xk, Xo (Xi⁺, Xk⁺, and Xo⁺). Within this last group, there is the *grimshawi* species group, characterized by the

standard fourth chromosomal sequence and the *glabriapex* species group. Within both these latter groups, several species complexes are poorly resolved by analysis of the chromosomal banding patterns (see below).

To determine taxonomic relationships within the *grimshawi* species group, we used all 38 representatives of the group: *Drosophila affinisdisjuncta*, *D. atrimentum*, *D. balioptera*, *D. bostrycha*, *D. ciliaticrus*, *D. claytonae*, *D. crucigera*, *D. disjuncta*, *D. engyochracea*, *D. flexipes*, *D. formella*, *D. gradata*, *D. grimshawi*, *D. gymnobasis*, *D. hawaiiensis*, *D. heedi*, *D. hirtipalpus*, *D. lasiopoda*, *D. limitata*, *D. mulli*, *D. murphyi*, *D. musaphilia*, *D. obatai*, *D. ochracea*, *D. orphnopeza*, *D. orthofascia*, *D. psilotarsalis*, *D. pullipes*, *D. recticilia*, *D. reynoldsiae*, *D. sejuncta*, *D. silvarentis*, *D. sobrina*, *D. sodomae*, *D. sproati*, *D. turbata*, *D. villitibia*, and *D. villosipedis*. *Drosophila punalua* was used as an outgroup. A heuristic search generated six trees, length 46, which were then weighted according to the RC and reanalyzed. The result was the same set of six trees, with a CI of 1.000 and an RI of 1.000. There were nine terminal chromosomal groupings, represented in Figure 5.1 by *D. ciliaticrus*, *D. engyochracea*, *D. flexipes*, *D. gradata*, *D. grimshawi*, *D. hawaiiensis*, *D. hirtipalpus*, *D. murphyi*, and *D. ochracea*.

To determine the phylogenetic structure within the *glabriapex* species group, we used the remaining 33 species that were not included in the *grimshawi* species group: *Drosophila aglaia*, *D. alsophila*, *D. assita*, *D. basisetae*, *D. conspicua*, *D. digressa*, *D. discreta*, *D. distinguenda*, *D. divaricata*, *D. fasciculisetae*, *D. glabriapex*, *D. gymnophallus*, *D. hexachaetae*, *D. inedita*, *D. lineosetae*, *D. liophallus*, *D. macrothrix*, *D. micromyia*, *D. montgomeryi*, *D. ocellata*, *D. odontophallus*, *D. paucicilia*, *D. paucipuncta*, *D. pilimana*, *D. prolaticilia*, *D. prostopalpis*, *D. psilophallus*, *D. punalua*, *D. spaniothrix*, *D. tarphytrichia*, *D. uniseriata*, *D. vesciseta*, and *D. virgulata*. *Drosophila ornata* was used as an outgroup. A heuristic search generated four trees, length 67. Weighting according to the RC generated the same four trees, with a CI of 1.000 and an RI of 1.000. There were eight terminal chromosomal groupings, represented in Figure 5.1 by *Drosophila assita*, *D. discreta*, *D. distinguenda*, *D. glabriapex*, *D. gymnophallus*, *D. punalua*, *D. spaniothrix*, and *D. virgulata*.

Relationships among species in the *planitibia* clade were determined using all 17 representatives of the clade: *Drosophila cyrtoloma*, *D. differens*, *D. hanaulae*, *D. hemipeza*, *D. heteroneura*, *D. ingens*, *D. melano-*

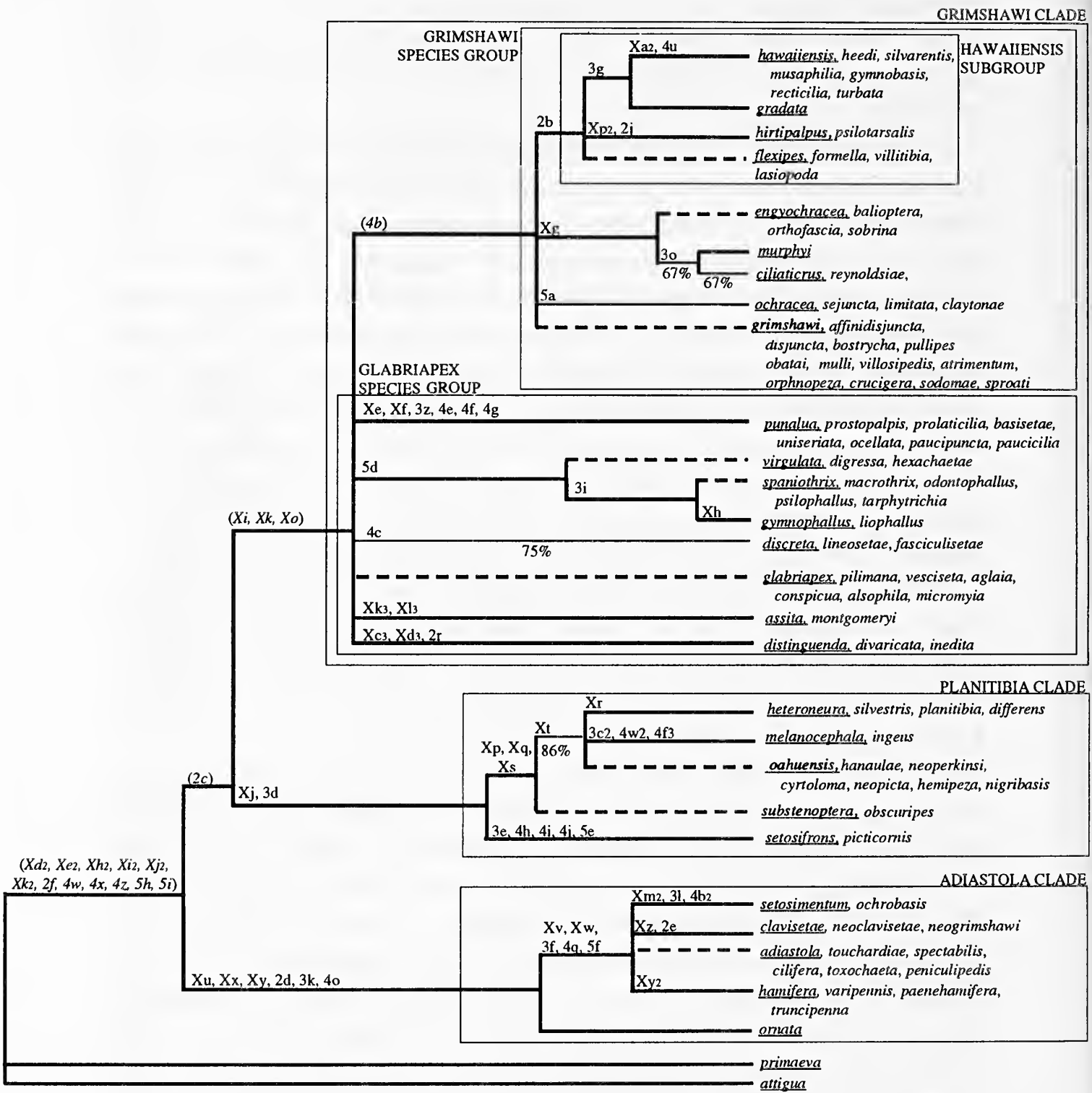


FIGURE 5.1. Phylogeny of 106 species of picture-winged Hawaiian *Drosophila*. All resolved nodes have 100% support, except for the four marked. *Solid lines* lead to terminal groupings supported by specific chromosomal rearrangements, using the terminology of Carson (1992). All marked characters indicate chromosomal inversion gains relative to the “standard” *D. grimshawi*, except for those in parentheses and in italics, such as (4b), which indicate an inversion loss. *Dashed lines* lead to groups of taxa within which relationships are unresolved and that do not form distinct groupings. Terminal taxa that are underlined are those chosen to represent groups of species that are homosequential with the terminal taxon or that differ from it by autapomorphic character(s) only.

cephala, *D. neoperkinsi*, *D. neopicta*, *D. nigribasis*, *D. oahuensis*, *D. obscuripes*, *D. picticornis*, *D. planitibia*, *D. setosifrons*, *D. silvestris*, and *D. substenoptera*. *Drosophila ornata* was used as an outgroup. A heuristic search generated 28 trees, length 59, which were then weighted according to the RC and reanalyzed. The result was again 28 trees, with a CI of 1.000 and an RI of 1.000. There were five terminal chromosomal groupings, represented in Figure 5.1 by *D. heteroneura*, *D. melanocephala*, *D. oahuensis*, *D. setosifrons*, and *D. substenoptera*.

To establish the structure within the *adiastola* clade, we used all 16 representatives of the clade: *Drosophila adiaastola*, *D. cilifera*, *D. clavisetae*, *D. hamifera*, *D. neoclavisetae*, *D. neogrimshawi*, *D. ochrobasis*, *D. ornata*, *D. paenehamifera*, *D. peniculipedis*, *D. setosimentum*, *D. spectabilis*, *D. touchardiae*, *D. toxochaeta*, *D. truncipenna*, and *D. varipennis*. *Drosophila primaeva* was used as an outgroup. A heuristic search generated three trees, length 75. Weighting according to the RC generated the same three trees, with a CI of 0.991 and an RI of 0.963. There were five terminal chromosomal groupings, represented in Figure 5.1 by *D. adiaastola*, *D. clavisetae*, *D. hamifera*, *D. ornata*, and *D. setosimentum*.

Classical sibling species typically show fixed inversion differences. A feature of the Hawaiian drosophilids is the existence of 19 groups of chromosomally homosequential species that are nevertheless morphologically distinguishable (Carson et al., 1967). In other cases, the number of fixed inversion differences characterizing species of picture-winged Hawaiian *Drosophila* is quite variable. Some species may differ from their closest relatives by a single inversion, others are separated by two or more inversions, and so on. In general, the more derived species have fewer fixed inversions separating representatives (e.g., less than five inversions separate species in the *hawaiiensis* subgroup), whereas more ancestral species are characterized by many fixed differences (e.g., *D. ornata* from the island of Kaua'i is separated from *D. setosimentum* from the island of Hawai'i by 18 fixed inversions). The two most ancestral species, *D. primaeva* and *D. attigua*, differ from each other by 13 fixed inversions.

The fact that there are so many species that show identical banding patterns in the polytene chromosomes indicates that speciation is not necessarily accompanied by fixation of paracentric inversions. Indeed, inversions probably arise in clusters, under the influence of transposable elements (Carson, 1992b).

THE EXTERNAL MALE GENITALIA

Sturtevant (1919) first mentioned the significance of the external male genitalia of *Drosophilidae* as a taxonomic tool for distinguishing between closely related species. Indeed, in cases of sibling species in which other external morphological characters are extremely similar, taxonomists have often had to rely on detailed comparisons of the structures of the male genitalia for distinguishing sibling species. Snodgrass (1957) stated that "the great diversity in structural detail of the genitalia gives these organs a value for identification of insect species almost equal to that of fingerprints for identification of human individuals." Indeed, Hardy (1965) showed that the structures of the complex male genitalia of *Scaptomyza* species in the Hawaiian Islands are extremely important for differentiating between closely related species. For the most part, other external features (i.e., nongenitalic) of *Scaptomyza* species have been very conservative in the evolutionary history of these species and have not been useful for species identification. However, Kaneshiro (1969) observed that the male genitalia of the Hawaiian *Drosophila* species were not particularly useful for separating closely related species. Rather, he found that the strong similarities in the phallic organs, especially that of the penis, were extremely useful in showing phylogenetic relationships among many species of the large picture-winged group.

Kaneshiro (1974) suggested that the dichotomy in the usefulness of the male genitalia for distinguishing species in *Scaptomyza* versus those in *Drosophila* may be correlated with the differences in mating behavior between the two groups. In *Drosophila* species, the males perform complex courtship displays before attempting to mount the female. Once the female provides an acceptance signal, the male mounts the female and, occasionally, copulation ensues. However, courtship can continue for several minutes, and in most cases, the female rejects the overtures of the male either by leaving the courtship arena or by physically aggressing against the male, inducing him to depart. Therefore, sexual selection in *Drosophila* appears to occur before the male mounting the female, explaining the elaborate secondary sexual structures observed in the external morphology of males of many of the species in this group. The species in the genus *Scaptomyza*, however, display an assault-type courtship behavior with minimal premounting display. The males approach the female and immediately mount the female. In the mounted position, the male appears to remain motionless while performing many tactile stimuli involving the complex genitalic structures. Thus, in *Scaptomyza*, sexual

selection appears to occur at the level of tactile stimuli from the male genitalia presumably with corresponding receptors in the female genitalia (ovipositor plates).

SUBGROUPINGS BASED ON EXTERNAL MALE GENITALIA

Based on comparisons of the external male genitalia, Kaneshiro (1969) formed subgroups that agree, in general, with the groupings based on chromosomal analyses. Nevertheless, the genitalic study provided, in many cases, a greater resolution in separating the species within the larger species groups into species subgroups (Table 5.1). For example, the *grimshawi* species group can be subdivided into three species subgroups, the *grimshawi* subgroup (7 species), the *orphnopeza* subgroup (17 species), and the *hawaiiensis* subgroup (14 species).

The *glabriapex* species group can be differentiated into the *glabriapex* subgroup (five species), the *punalua* subgroup (eight species), the *vesciseta* subgroup (eight species), the *conspicua* subgroup (nine species), and the *distinguenda* subgroup (three species).

Some species can be placed in different groups based on comparisons of the aedeagus even though they are all chromosomally homosequential. For example, 13 homosequential species can be divided into the *grimshawi* subgroup (*D. affinidisjuncta*, *D. bostrycha*, *D. crucigera*, *D. disjuncta*, and *D. grimshawi*) and the *orphnopeza* subgroup (*D. atrimentum*, *D. mulli*, *D. obatai*, *D. orphnopeza*, *D. pullipes*, *D. sodomae*, *D. sproati*, and *D. villosipedis*). There are also some discrepancies between chromosomal and morphological data. For example, among four homosequential species, *D. aglaia*, *D. glabriapex*, *D. pilimana*, and *D. vesciseta*, *D. vesciseta* appears to be more closely related to *D. assita* and *D. micromyia* based on comparisons of the male genitalia even though they are two and four fixed inversions removed from *D. vesciseta*, respectively. *Drosophila pilimana* and *D. glabriapex* are more closely related to *D. discreta*, *D. lineosetae*, and *D. fasciculisetæ*, which have as many as four fixed inversion differences. *Drosophila aglaia* appears to be more closely related to *D. conspicua*, which is three fixed inversions removed.

The point here is that although the genitalic information appears to agree well with the chromosomal phylogeny for higher-level group or clade designations, a comparative study of the external male genitalia can often resolve the groupings into species subgroups. In cases of chromo-

TABLE 5.1. Hawaiian *Drosophila* Species Group and Subgroup Relationships Based on External Male Genitalia

| Clade | Species group | Species subgroup | Species |
|-------------------------------------|-------------------------------------|--|--|
| <i>primaeva</i> <i>adiastola</i> | <i>primaeva</i> <i>adiastola</i> | <i>primaeva</i> <i>adiastola</i> | <i>Drosophila primaeva</i> , <i>D. attigua</i> <i>D. adiaastola</i> , <i>D. cilifera</i> , <i>D. peni-</i> <i>culipedis</i> , <i>D. ochrobasis</i> , <i>D. seto-</i> <i>simentum</i> , <i>D. spectabilis</i> , <i>D.</i> <i>touchardiae</i> , <i>D. toxochaeta</i> , <i>D.</i> <i>ornata</i> , <i>D. clavisetae</i> , <i>D.</i> <i>neoclavisetae</i> , <i>D. neogrimshawi</i> |
| | | <i>truncipenna</i> | <i>D. truncipenna</i> , <i>D. hamifera</i> , <i>D.</i> <i>varipennis</i> , <i>D. paenehamifera</i> |
| <i>planitibia</i> | <i>planitibia</i> | <i>planitibia</i> | <i>D. planitibia</i> , <i>D. differens</i> , <i>D.</i> <i>silvestris</i> , <i>D. heteroneura</i> , <i>D.</i> <i>hemipeza</i> |
| | | <i>cyrtoloma</i> | <i>D. cyrtoloma</i> , <i>D. obscuripes</i> , <i>D.</i> <i>nigribasis</i> , <i>D. oahuensis</i> , <i>D.</i> <i>melanocephala</i> , <i>D. ingens</i> , <i>D.</i> <i>neoperkinsi</i> , <i>D. hanaulae</i> , <i>D.</i> <i>neopicta</i> , <i>D. substenoptera</i> |
| <i>grimshawi</i> | <i>grimshawi</i> | <i>picticornis</i> <i>grimshawi</i> | <i>D. picticornis</i> , <i>D. setosifrons</i> <i>D. grimshawi</i> , <i>D. crucigera</i> , <i>D.</i> <i>affinidisjuncta</i> , <i>D. disjuncta</i> , <i>D.</i> <i>bostrycha</i> , <i>D. balioptera</i> , <i>D.</i> <i>pullipes</i> |
| | | <i>orphnopeza</i> | <i>D. orphnopeza</i> , <i>D. mulli</i> , <i>D.</i> <i>villosipedis</i> , <i>D. atrimentum</i> , <i>D.</i> <i>sodomae</i> , <i>D. sproati</i> , <i>D. ochra-</i> <i>cea</i> , <i>D. sejuncta</i> , <i>D. limitata</i> , <i>D.</i> <i>claytonae</i> , <i>D. ciliaticrus</i> , <i>D.</i> <i>reynoldisae</i> , <i>D. engyochracea</i> , <i>D. orthofascia</i> , <i>D. sobrina</i> , <i>D.</i> <i>murphyi</i> , <i>D. obatai</i> |
| | | <i>hawaiiensis</i> | <i>D. hawaiiensis</i> , <i>D. heedi</i> , <i>D.</i> <i>silvarentis</i> , <i>D. musaphilia</i> , <i>D.</i> <i>gymnobasis</i> , <i>D. recticilia</i> , <i>D.</i> <i>turbata</i> , <i>D. gradata</i> , <i>D. hirti-</i> <i>palpus</i> , <i>D. psilotarsalis</i> , <i>D. flexi-</i> <i>pipes</i> , <i>D. formella</i> , <i>D. villitibia</i> , <i>D.</i> <i>lasiopoda</i> |
| | <i>glabriapex</i> | <i>glabriapex</i> | <i>D. glabriapex</i> , <i>D. pilimana</i> , <i>D. dis-</i> <i>creta</i> , <i>D. fasciculisetae</i> , <i>D. lineo-</i> <i>setae</i> |

(Continued)

TABLE 5.1. (Continued)

| Clade | Species group | Species subgroup | Species |
|-----------------------------|------------------------------|---------------------|---|
| <i>grimshawi</i> (cont.) | <i>glabriapex</i> (cont.) | <i>punalua</i> | <i>D. punalua</i> , <i>D. prostopalpis</i> , <i>D. prolaticilia</i> , <i>D. basisetae</i> , <i>D. uniseriata</i> , <i>D. ocellata</i> , <i>D. paucipuncta</i> , <i>D. paucicilia</i> |
| | | <i>vesciseta</i> | <i>D. vesciseta</i> , <i>D. alsophila</i> , <i>D. as-sita</i> , <i>D. micromyia</i> , <i>D. montgomeryi</i> , <i>D. virgulata</i> , <i>D. digressa</i> , <i>D. hexachaetae</i> |
| | | <i>conspicua</i> | <i>D. conspicua</i> , <i>D. aglaia</i> , <i>D. spaniothrix</i> , <i>D. macrothrix</i> , <i>D. odontophallus</i> , <i>D. psilophallus</i> , <i>D. tarphytrichia</i> , <i>D. gymno-phallus</i> , <i>D. liophallus</i> |
| | | <i>distinguenda</i> | <i>D. distinguenda</i> , <i>D. divaricata</i> , <i>D. inedita</i> |

somally homosequential species, the external male genitalia provide additional information with which the species can be separated into clearly marked species subgroups. The examples described above illustrate the significance of applying a combination of taxonomic criteria for interpreting phylogenetic relationships among related species.

GEOGRAPHIC DISTRIBUTION OF THE
PICTURE-WINGED DROSOPHILA

We have generated an area cladogram based on the chromosomal data of the picture-winged *Drosophila* (Figure 5.2). This area cladogram is not directly comparable to the others in this volume because it treats species groups rather than individual taxa. Despite this, several general points can be made. The absence of chromosomal rearrangements at lower taxonomic levels suggests that these rearrangements are not involved in initial species divergence. There are 24 clades with two or more species: 20 of these are found on two or more islands, and only 4 are found on a single island, one group (three species) on O‘ahu and two groups (two and three species) on Maui and one group (two species) on Hawai‘i. This pattern is in apparent agreement with the results of DeSalle (this volume,

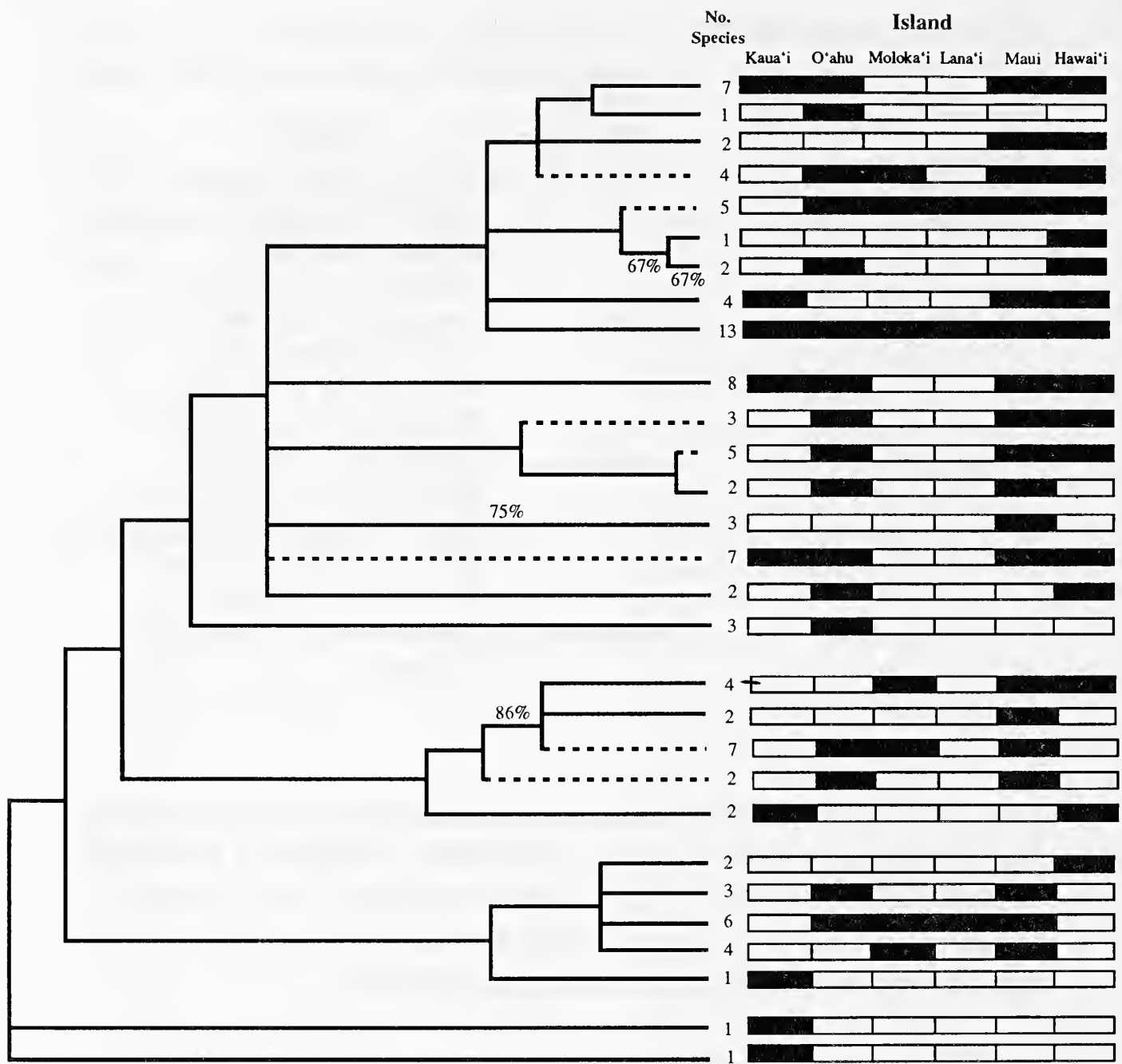


FIGURE 5.2. General area cladogram of Hawaiian *Drosophila* based on chromosomal types. For any given clade, the ancestral species tend to be on Kaua'i or O'ahu. The lack of chromosomal resolution at lower taxonomic levels suggests that chromosomal rearrangements are not involved in initial species divergence. Solid bar indicates presence on an island.

Chapter 6), who found that each lineage of flies he examined had an inter-island distribution pattern rather than a radiation on a single island. Of the 29 terminal taxa, only 6 of the nonbasal ones have species on Kaua'i. This also agrees with DeSalle's findings; all six of his clades were distributed from O'ahu to the younger islands, and none of them had species on Kaua'i. Three of the basal groups, however, are on Kaua'i, so when the area cladogram is optimized, it gives a Kaua'i ancestor for the

entire clade. The lack of resolution in the area cladogram and the fact that nearly all the clades are found on several islands is consistent with the pattern produced by many repeated introductions from older to younger islands.

The results of this analysis do not conflict with the results of other studies in this volume. Also, they indicate that there are 10 clades of four or more species that have interesting distributional patterns that should be studied at the species level as soon as possible. These clades have the potential to establish whether the individual clades follow an older-to-younger island dispersal pattern and help to investigate whether there is repeated dispersal from older islands.

Despite the lack of resolution of the chromosomal phylogeny, we have reliable data on the geographic distribution of the individual species of certain groups, especially the large picture-winged species, on the basis of extensive field work carried out during the many years of the Hawaiian *Drosophila* project, as well as the close scrutiny of the systematics and species identification of all specimens captured. Most of these species, like many other extant terrestrial endemic fauna, show a very strong but by no means exclusive tendency to single-island endemism. Most species thus appear to evolve on an island early in its history and thereafter remain confined to that island. Colonists arriving at newer emerging islands tend to form new species, a finding that has led to the serious consideration that speciation may be somehow related to founder events (see Carson, 1990a, for discussion). These results are particularly relevant, especially in view of the new information revealing that most of the older, presently low, islands northwest of Kaua'i were once high islands comparable in size to the present high islands (see Carson and Clague, this volume, Chapter 2). Accordingly, it seems clear that as each new island on the moving Pacific tectonic plate rose by volcanic action above sea level, new populations became established from colonists stemming from the older, sinking islands.

The important point is that these "founding" events have resulted in speciation on successively younger islands. Thus, active evolution, manifested by novel species and adaptations, has been most apparent at the newer, ecologically open lava flows that currently characterize the southeastern end of the archipelago.

6 Molecular Approaches to Biogeographic Analysis of Hawaiian Drosophilidae

ROB DESALLE

Biogeographic patterns can be examined at several hierarchical levels using the Hawaiian Drosophilidae. The complexity of the patterns roughly coincides with the particular taxonomic levels of these flies. The overall phylogenetic relationships of flies endemic to the archipelago to flies living in continental areas can best be examined at the generic and subgeneric levels in the family Drosophilidae. The biogeographic relationships of species on the various islands in the archipelago can be examined at the specific or infraspecific level. Possible relationships of areas within an island are best examined using populations within a species. This study examines these three levels from a molecular perspective and attempts to detect biogeographic patterns at these levels using mitochondrial DNA (mtDNA).

The first level concerns the origin of the Hawaiian Drosophilidae. Several authors have speculated on the origin of these flies. All have attempted to single out one or a few continental groups that might be the sister group of the Hawaiian lineage. Chromosomal (Stalker, 1972; Yoon, 1989; Carson, 1992b), behavioral (Spieth, 1982; Kaneshiro and Boake, 1987), morphological (Hardy, 1965; Throckmorton, 1966; Carson and Kaneshiro, 1976; Grimaldi, 1990), and recently, molecular techniques (Beverley and Wilson, 1985; Thomas and Hunt, 1991; DeSalle, 1992) have been used to examine this question.

The second level concerns the detection of biogeographic patterns within the Hawaiian archipelago. These patterns will most likely reflect

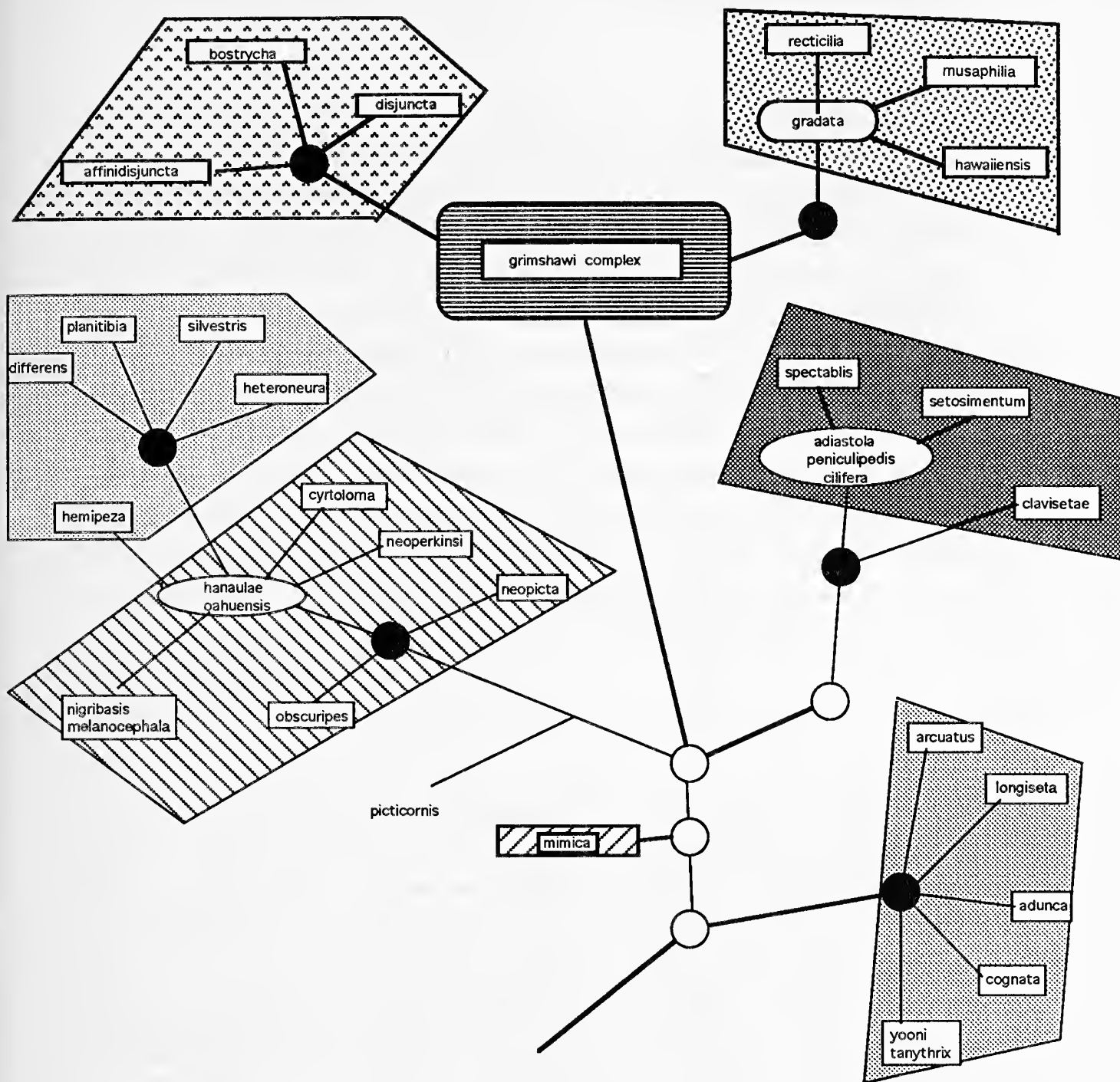


FIGURE 6.1. Diagram showing the chromosomal relationships of the taxa examined in this study. The *filled-in circles* indicate the relevant chromosomal ancestor that determines the monophyly of the species in each group.

inter-island founder events and have previously been examined from ecological and chromosomal data. The chromosomal data (Carson, 1987b, 1992b) are probably the most enlightening for the examination of biogeographic patterns at this level. Several species groups exist within the Hawaiian picture-winged drosophilids that are ideal for this level of biogeographic analysis (Figure 6.1).

The final level concerns the detection of biogeographic patterns within an island. Hawai'i, the youngest of the current high islands in the

archipelago, allows for the examination of patterns at this level. In particular, *Drosophila silvestris* resides in most of the rainforests that ring the island of Hawai'i. Previous analyses of *D. silvestris* populations using morphological (Carson et al., 1982), chromosomal (Craddock and Carson, 1989), and isozyme (Craddock and Johnson, 1979) techniques were able to detect a pattern of basal populations on the western side of the island and more derived populations on the eastern side of the island (Carson, 1992b). Kaneshiro and Kurihara (1981) used behavioral studies to establish mating asymmetries that they interpreted as showing biogeographic patterns between areas from both sides of Hawai'i. DeSalle and Templeton (1992) examined the relationship of *D. silvestris* populations on the eastern side of the island of Hawai'i using molecular techniques and observed the same overall patterns for this side of the island as Kaneshiro and Kurihara (1981).

MATERIALS AND METHODS

The biogeographic relationship of *Drosophila* in the Hawaiian archipelago with those of continental areas has been examined in DeSalle (1992) using the 16S rDNA and ND-1 mtDNA sequences. Information for a more limited number of taxa for alcohol dehydrogenase sequences exists (Thomas and Hunt, 1991; DeSalle, 1992) and is also mentioned here. Parsimony trees were generated using PAUP version 3.0j (Swofford, 1990a). Hypotheses about the sister-group relationships of the Hawaiian taxa were examined, and an area cladogram was constructed. Because of the large number of taxa in some of the analyses, heuristic searches using a random addition option were performed.

The taxa and outgroups for the study of the biogeographic relationships of six species groups among islands in the Hawaiian archipelago were chosen on the basis of chromosomal data. Only those groups of flies that were shown to be a monophyletic group on the basis of chromosomal inversions were used. Outgroups were always outside of these monophyletic groups on the basis of chromosomal data. Six groups of *Drosophila* and their outgroups were identified that fit these criteria (Figure 6.1, Table 6.1). Character state data were obtained in the form of mtDNA restriction fragment length polymorphisms (RFLPs). These data were collected using the methods outlined in DeSalle et al. (1986b) and DeSalle and Giddings (1986). For most data sets, at least nine restriction enzymes were used to collect character state information. These restric-

TABLE 6.1. *Drosophila* Species Used in the Inter-island Biogeographic Analysis

| Species group or subgroup | Species | Abbreviation ^a | Outgroup ^b |
|---|---------------------------|---------------------------|-----------------------|
| <i>antopocerus</i> | <i>D. yooni</i> | yoon | <i>D. arcuatus</i> |
| | <i>D. cognata</i> | cogn | |
| | <i>D. tanythrix</i> | tany | |
| | <i>D. adunca</i> | adun | |
| | <i>D. longiseta</i> | long | |
| | <i>D. arcuatus</i> | arcu | |
| Picture-winged <i>hawaiiensis</i> | <i>D. hawaiiensis</i> | hawi | <i>D. musaphilia</i> |
| | <i>D. gradata</i> | grad | |
| | <i>D. recticilia</i> | rect | |
| | <i>D. musaphilia</i> | musa | |
| Picture-winged <i>adiastola</i> | <i>D. adiaastola</i> | adia | <i>D. clavisetae</i> |
| | <i>D. setosimentum</i> | seto | |
| | <i>D. clavisetae</i> | clav | |
| | <i>D. cilifera</i> | cili | |
| | <i>D. spectabilis</i> | spec | |
| | <i>D. peniculipedis</i> | peni | |
| Picture-winged <i>affinidisjuncta</i> | <i>D. affinidisjuncta</i> | affi | <i>D. grimshawi</i> |
| | <i>D. bostrycha</i> | bost | |
| | <i>D. disjuncta</i> | disj | |
| | <i>D. grimshawi</i> | grim | |
| Picture-winged alpha <i>planitibia</i> | <i>D. cyrtoloma</i> | cyrt | <i>D. picticornis</i> |
| | <i>D. melanocephala</i> | mcph | |
| | <i>D. hanaulae</i> | hana | |
| | <i>D. neoperkinsi</i> | npki | |
| | <i>D. obscuripes</i> | obsc | |
| | <i>D. nigribasis</i> | nigb | |
| | <i>D. oahuensis</i> | oahu | |
| | <i>D. neopicta</i> | npct | |
| | <i>D. silvestris</i> | silv | |
| Picture-winged beta <i>planitibia</i> | <i>D. heteroneura</i> | hete | <i>D. neopicta</i> |
| | <i>D. planitibia</i> | plan | |
| | <i>D. differens</i> | diff | |
| | <i>D. hemipeza</i> | hemi | |
| | <i>D. neopicta</i> | npct | |

^aUsed in Appendix 6.1.
^bUsed in the individual analyses.



FIGURE 6.2. Study areas for the inter-island analysis of six lineages of *Drosophila*. Area abbreviations are K, Kaua'i; O, O'ahu; MK, Moloka'i; ME1, East Maui (Waikamoi); ME2, East Maui (Paliku); MW, West Maui (Hana'ula); HH, Hawai'i (Hilo side); HK, Hawai'i (Kona side).

tion enzymes varied from study to study. Restriction sites were mapped and scored as present or absent to generate the character state data. Parsimony trees were generated from the data sets for each species subgroup listed in Table 6.1 using PAUP (Swofford, 1990a). The areas examined in this study are summarized in Figure 6.2. Area cladograms were then constructed from the taxon cladograms (Page, 1988, 1989). Because all the species in these analyses are single-island endemics, the analyses of these six groups are straightforward due to the lack of both widespread taxa and missing areas.

The characters for the study of biogeographic relationships of *Drosophila silvestris* populations within the island of Hawai'i are described in detail in DeSalle and Templeton (1992) and DeSalle et al. (1986a). Thirty-three characters are included from mapped four-base cutter enzymes (23 characters), several DNA sequence characters from ND-1, ND-2, and ND-5 mtDNA genes (2 characters), and characters from six-base cutter enzymes (8 characters). Taxon parsimony trees for the population level data were generated using PAUP. Area cladograms were constructed directly from the taxon cladogram using COMPONENT (Page, 1989) under assumptions 0, 1, and 2. These assumptions refer to the treatment of missing areas, widespread taxa, and redundant distributions in biogeographic analysis. Component analysis under assumption 0 is considered a valid approach if the taxa under examination are neither widespread nor show redundant distributions (i.e., if the taxa are entirely endemic to single areas). If there are widespread taxa or redundant distributions with respect to the areas under examination, then assumptions 1 and 2 are the more suitable approaches. Assumption 0 is the most prohibitive of the three assumptions with respect to the number of area cladograms allowed. Consequently, area relationships generated under assumption 0 will often show more resolution than under assumptions 1

and 2. Assumption 1 is more prohibitive with respect to the number of cladograms than assumption 2. For a more detailed discussion of these assumptions, see Nelson and Platnick (1981) and Page (1988, 1990).

RESULTS

Origin of the Hawaiian Drosophilidae

The Hawaiian Drosophilidae are monophyletic. There is no single continental form that can be designated as the sister to the Hawaiian lineages. The analysis for this level of biogeographic pattern is essentially the same as in DeSalle (1992). Taxa from the three main genera of Hawaiian Drosophilidae (Hawaiian *Scaptomyza*, Hawaiian *Drosophila* [or *Idiomyia*, Grimaldi, 1990] and *Engiscaptomyza*) were used to represent the Hawaiian lineages. Figure 6.3A shows the phylogenetic analysis using mtDNA sequences and 11 continental Drosophilidae candidates. Figure 6.3B shows a total evidence analysis in which both Adh and mtDNA sequence data were combined for those taxa that were common to both studies. The pattern that emerges in these phylogenetic analyses addresses three important points. First, the three distinct taxonomic lineages of Hawaiian *Drosophila* (or *Idiomyia*, Grimaldi, 1990) and *Engiscaptomyza* comprise a monophyletic group in both analyses depicted in Figure 6.3. Second, *Hirtodrosophila*, the only non-*Drosophila* candidate for sister-group status to the Hawaiian *Drosophila* (Grimaldi, 1990), is shown to be basal in both analyses, as Grimaldi's (1990) analysis also shows. Third, there is no single continental species or species group that can clearly be designated as sister to the monophyletic Hawaiian lineage. Inclusion of extra-Hawaiian *Scaptomyza* taxa in an analysis, which was not done here, could alter the tree topologies reported in this analysis.

Biogeographic Patterns of *Drosophila* within the Hawaiian Islands

The six species groups of Hawaiian *Drosophila* examined produce roughly similar inter-island phylogenetic patterns. Appendix 6.1 shows the data used for these analyses. The phylogenetic patterns that arise from these data (Figure 6.4) indicate a general trend of the most basal taxa occurring in the rainforests of the older or central islands in the archipelago (O'ahu or Moloka'i), with the more derived taxa residing in the younger islands (usually Hawai'i). Tree statistics obtained from parsimony analysis are shown in Table 6.2.

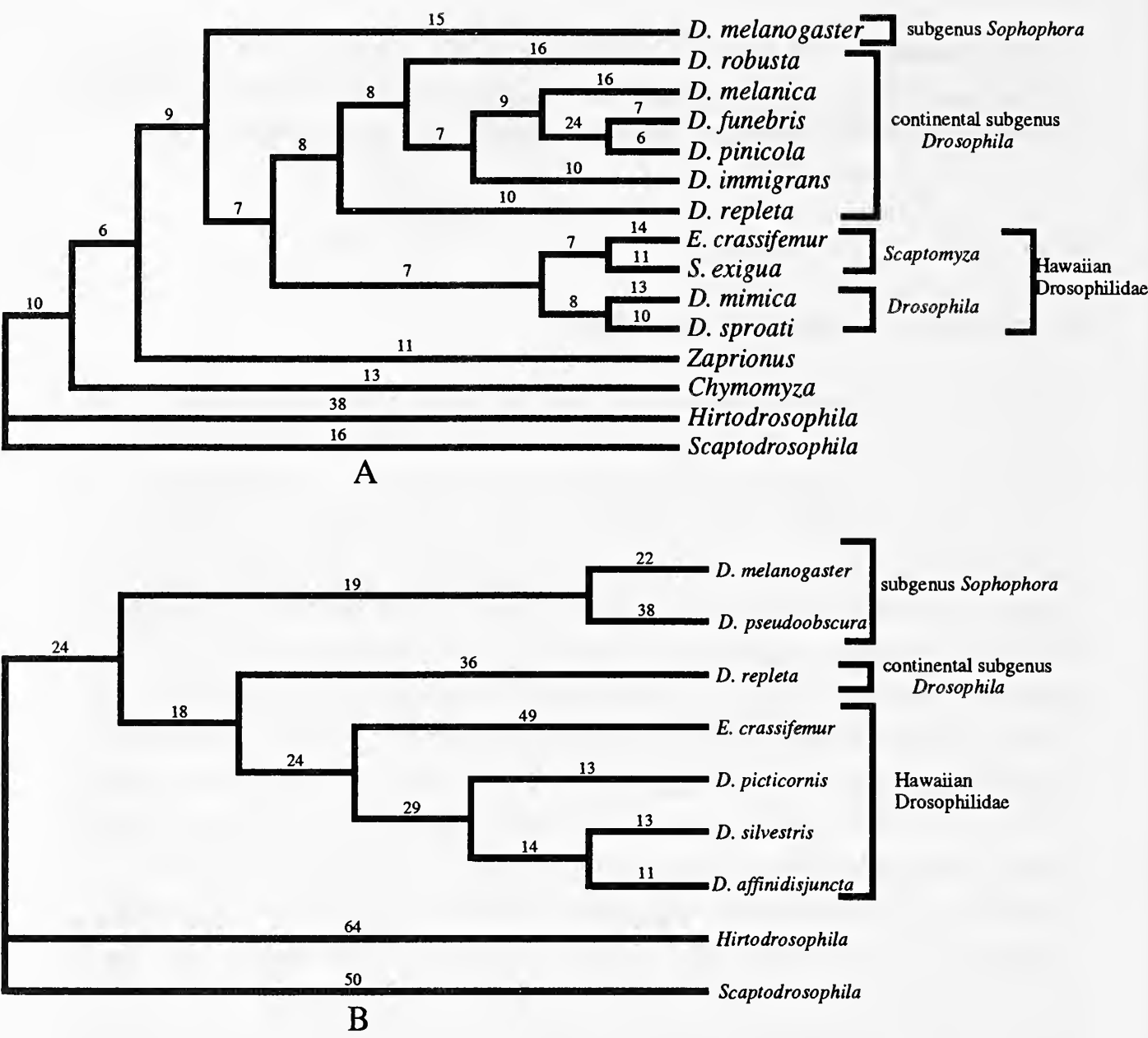


FIGURE 6.3. (A) mtDNA phylogeny of 11 continental Drosophilidae and 4 Hawaiian species. Numbers on the cladogram branches indicate the length of the branch. (B) Total evidence tree for nine Drosophilidae in which 905 bases of mtDNA data and 238 bases of Adh sequence exist. The limits of the Adh sequences coincide with those reported in DeSalle (1992). Numbers on the cladogram branches indicate the length of the branch.

The patterns observed in these cladograms were used to construct area cladograms for each species group and subgroup (see Figure 6.3). Construction of area cladograms requires the consideration of several aspects of the areas and taxa involved. The methodology for construction of area cladograms uses three assumptions (0, 1, and 2). Assumptions 1 and 2 differ from assumption 0 in how they interpret widespread taxa and redundant distributions. In particular, assumptions 1 and 2 incorporate the existence of widespread taxa and redundant distributions into the

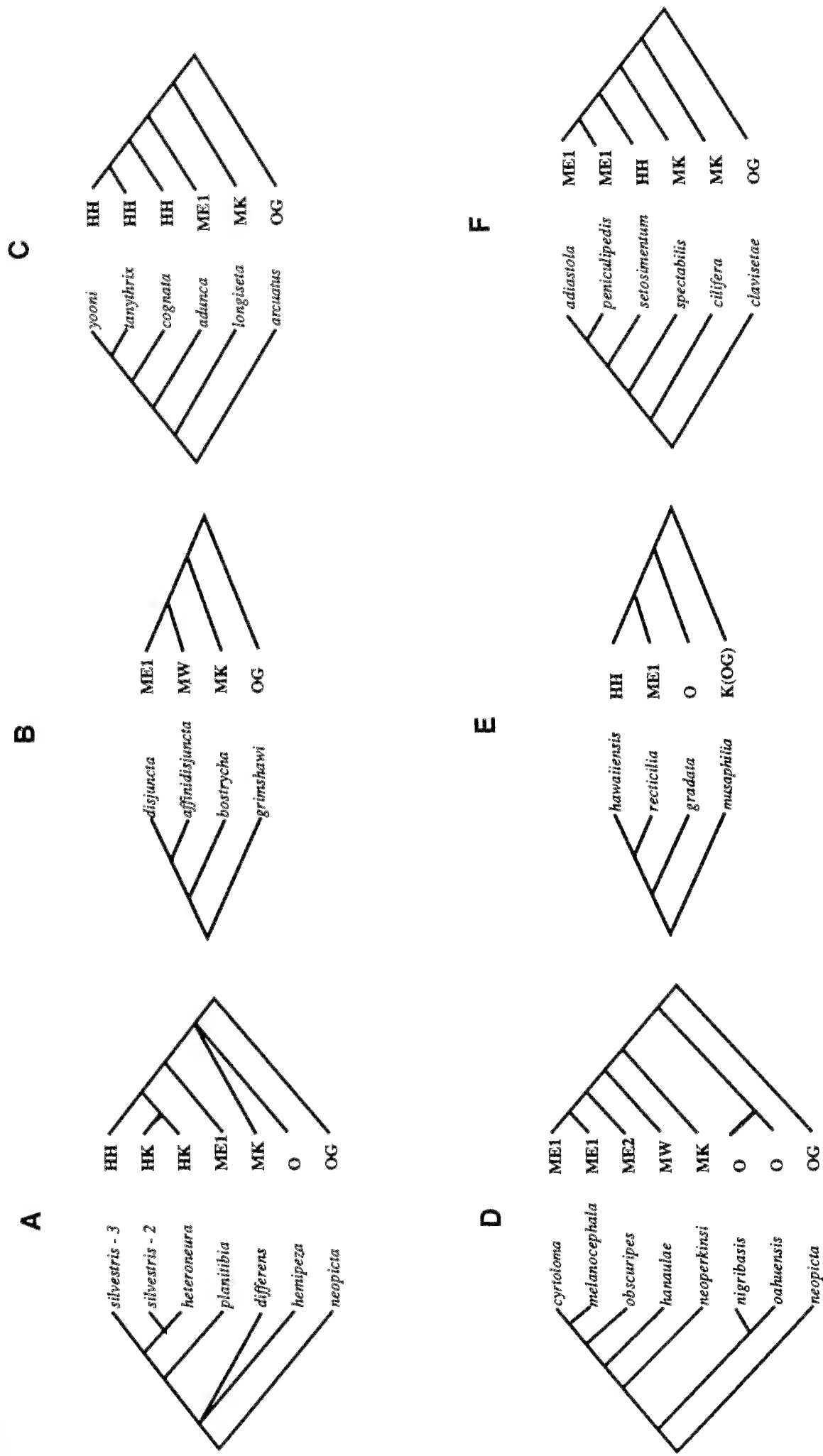


FIGURE 6.4. mtDNA cladograms on the left and area cladograms on the right. Area abbreviations are OG, outgroup; K, Kaua'i; O, O'ahu; MK, Moloka'i; ME1, East Maui (Waikamoi); ME2, East Maui (Paliku); MW, West Maui (Hana'ula); HH, Hawai'i (Hilo side); HK, Hawai'i (Kona side). (A) *planitibia*; (B) *affinidisjuncta*; (C) *antopocerus*; (D) alpha *planitibia*; (E) *hawaiiensis*; (F) *adiastola*.

TABLE 6.2. Tree Statistics for Individual Data Sets

| Species group or subgroup | CI | RI | Steps |
|--|----|----|-------|
| <i>antopocerus</i> | 91 | 91 | 44 |
| Picture-winged <i>hawaiiensis</i> | 80 | 75 | 20 |
| Picture-winged <i>adiastola</i> | 60 | 51 | 71 |
| Picture-winged <i>affinidisjuncta</i> | 67 | 50 | 32 |
| Picture-winged alpha <i>planitibia</i> | 62 | 59 | 99 |
| Picture-winged beta <i>planitibia</i> | 63 | 61 | 89 |

Notes: CI, consistency index; RI, retention index; steps, number of steps in the tree including uninformative characters. CI and RI were computed ignoring uninformative characters.

construction of area cladograms. Because all the taxa used to construct area cladograms for the separate Hawaiian species groups and subgroups are single-island endemics with no redundancy in distribution, the problem of constructing a general area cladogram collapses to assumption 0. What this means becomes evident when these data are analyzed using COMPONENT (Page, 1989) because generally all three assumptions give the same area cladograms.

A matrix with the relevant information for construction of a general area cladogram from the analyses of the six species groups and subgroups is shown in Appendix 6.2. The resulting area cladogram from this data matrix (Figure 6.5) indicates that the islands of O‘ahu and Moloka‘i were most likely areas of original endemism for these taxa. The younger islands of Maui and Hawai‘i are observed as the islands on which more recent differentiation has occurred.

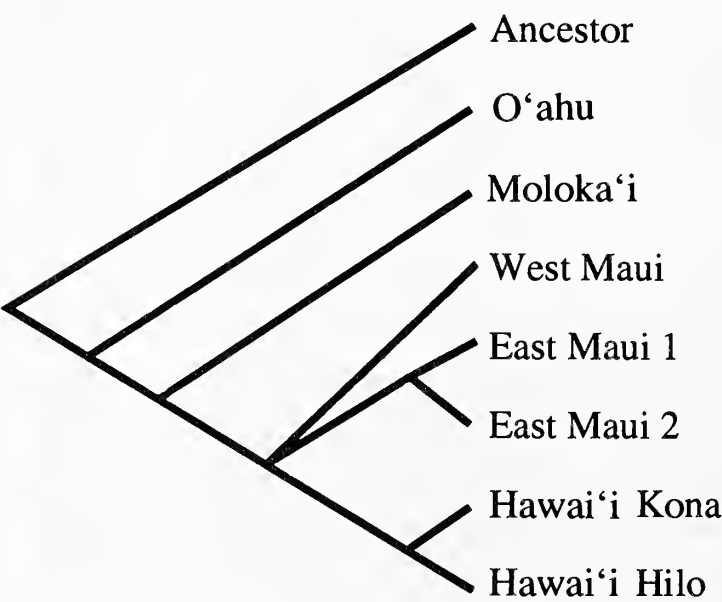


FIGURE 6.5. General area cladogram for the six lineages in Figure 6.4 using the matrix in Appendix 6.1.

Biogeographic Patterns in *Drosophila silvestris* on the Island of Hawai'i

An area cladogram for the eastern side of the island of Hawai'i was constructed using the data and analyses in DeSalle and Templeton (1992) and DeSalle et al. (1986a). In those studies, the congruence of the molecular cladogram with a behavioral hypothesis was the primary interest. The characters and character states are shown in Appendix 6.3. Area relationships for the eastern side of the island of Hawai'i can be obtained from these RFLP and DNA sequence data by constructing an area cladogram using COMPONENT (Page, 1989) under assumptions 0, 1, and 2 (due to redundant distributions of some lineages). The results of this analysis (Figure 6.6) indicate that there is a pattern of more derived populations and individuals on the southernmost part of the island, with the more basal populations residing on the northernmost part of the island.

DISCUSSION

General biogeographic patterns can be observed at several hierarchical levels in the Hawaiian Drosophilidae using different molecular tools. The molecular approaches described in this report vary from level to level. The origin of the diverse Hawaiian lineages from possible continental ancestors was approached using DNA sequences of a relatively slowly evolving region of the mtDNA (DeSalle, 1992) and a portion of the Adh gene (Thomas and Hunt, 1991; DeSalle, 1992). These gene regions appear to generate enough DNA sequence variability to resolve certain relationships. RFLP techniques were used to examine the other two hierarchical levels. Six-base cutter technology appears to be sensitive enough to detect patterns within species groups and subgroups. DNA sequences at this level, in general, generate nonsubstantial amounts of information in relation to effort (DeSalle et al., 1987). In fact, DNA sequences of two rapidly evolving mtDNA genes (ND-5 and ND-2) generated only two phylogenetically informative nucleotide positions among *Drosophila silvestris* populations (DeSalle and Templeton, 1992). Four-base cutters appear to be the most efficient means of generating molecular characters for within species questions in this study, as demonstrated by the analysis of *D. silvestris* populations (DeSalle and Templeton, 1992).

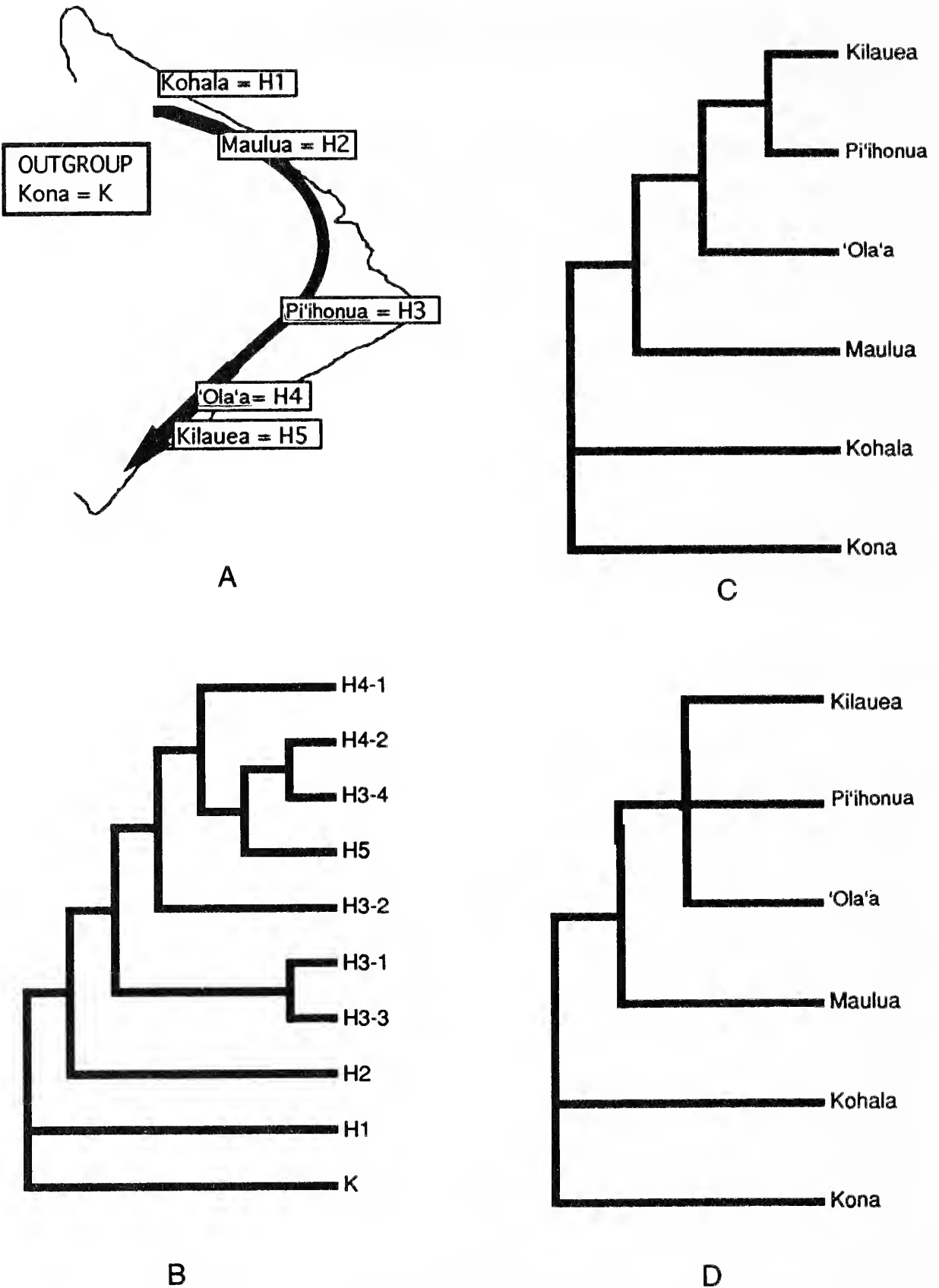


FIGURE 6.6. Area cladogram for intra-island analysis of *Drosophila silvestris* lineages. (A) Map of the east side of Hawai'i showing the areas examined in this study. The *arrow* indicates the direction of divergence established from the behavioral data of Kaneshiro and Kurihara (1981). (B) Taxon cladogram for the 10 individual isolines examined in this study. (C) Area cladogram under assumptions 0 and 1. (D) Area cladogram under assumption 2.

Origin of Hawaiian Drosophilidae

Three distinct questions can be asked to unravel the possible origin of the Hawaiian lineages. The first and most important point relevant to the validity of the other questions concerns the sister-group relationships of the Hawaiian taxa. Throckmorton (1966, 1975) first suggested that the Hawaiian taxa could be the product of a single or two introductions to the archipelago, primarily on the basis of internal morphological analysis. This conclusion stemmed from the existence of the Hawaiian drosophilid taxa (Hawaiian *Drosophila* or *Idiomyia*) and the Hawaiian scaptomyzoid (genus *Scaptomyza*) flies. If these two lineages are not sister taxa, then two or more continental groups may be sister to the Hawaiian Drosophilidae. Both DNA sequence data sets (Adh and mtDNA) support the notion that the Hawaiian *Drosophila* and Hawaiian *Scaptomyza* are sister taxa; thus, the next two questions can be approached under this hypothesis.

The second question concerns the relationship of the mycophagous clade of Drosophilidae that Grimaldi (1990) indicated as the sister group to the Hawaiian *Drosophila*. *Hirtodrosophila* was chosen as a representative of this group and, in these analyses, is shown to be basal in the drosophilid phylogeny, in agreement with Grimaldi's (1990) placement. The Hawaiian taxa are not seen as a sister group to the *Hirtodrosophila* (see Figure 6.3). Also, Grimaldi (1990) suggested that *Zaprionus* is the closest sister group to the Hawaiian *Scaptomyza* and *Engiscaptomyza*. This hypothesis also is not supported by the molecular data, as the Hawaiian *Scaptomyza* and *Engiscaptomyza* are placed well within the genus *Drosophila*.

The third question concerns the designation of a subgenus *Drosophila* or species group that could be the ancestor of the Hawaiian Drosophilidae. This question is best approached by placing several putative subgenus *Drosophila* candidates along with the Hawaiian Drosophilidae in a phylogenetic analysis (see Figure 6.3). The results of this analysis indicate that none of the continental subgenus *Drosophila* can be designated as the sole sister taxon of the Hawaiian lineages.

From these data, the Hawaiian *Drosophila* appears after *Hirtodrosophila* diverged from the ancestral drosophiline lineage and before the divergence of the major subgenus *Drosophila* species groups (see Figure 6.3). This observation, in effect, means that there is no single living taxon in the present analysis that can be assigned as the ancestor of the Hawaiian Drosophilidae. Amber fossil subgenus *Drosophila* and genus *Scaptomyza* (Grimaldi, 1987) of 30 million years ago (Ma) exist

that would give a minimum age of the divergence of the Hawaiian lineage from the subgenus *Drosophila* based on sister-group dating (Norell, 1992). This date of divergence is roughly similar to Beverley and Wilson's (1985) estimate of 40 Ma from a larval hemolymph protein "molecular clock" and from Thomas and Hunt's (1991) estimate of 20 Ma using an *Adh* molecular clock. These divergence times are interesting because they imply that the colonization of the Hawaiian archipelago could have occurred well before the origin of the current oldest Hawaiian Island (Kaua'i) that has sufficient rainforests to harbor these flies. This observation is not entirely surprising because the Hawaiian archipelago has been formed on a geologic "conveyor belt" (Carson and Kaneshiro, 1976; McKenna, 1983; Beverley and Wilson, 1985).

Inter-island Biogeographic Patterns

Most aspects of the mtDNA cladograms (see Figure 6.4) are in direct agreement with chromosomal data, but others show slight disagreement. For instance, the alpha sublineage of the *Drosophila planitibia* subgroup shows the two O'ahu species as ancestral. Carson (1987b) argued on the basis of chromosomal data that the area of origin for this lineage is actually the Maui Nui complex (Maui, Moloka'i, Lana'i, and Kaho'olawe) and that O'ahu members of this lineage arose as back-migrants. If this is correct, the patterns observed from mtDNA RFLP data might indicate that the back-migration events occurred very early in the differentiation of this clade.

The general area cladogram in Figure 6.5 clearly indicates that O'ahu is placed in the most basal position in the tree and that Moloka'i appears next. These two areas can therefore be interpreted as being established before the remaining three. The areas on Maui and Hawai'i are observed as sister areas and are the last areas to be established. A common misconception in the interpretation of these data would be to assume that vicariance events are responsible for the observed patterns. Endler (1982) argued that congruent area cladograms could reflect common ecological processes. Common dispersal pathways may also be reflected in congruent area cladograms (Endler, 1983; Page, 1988).

Intra-island Biogeographic Patterns

The big island of Hawai'i has also been formed as a consequence of the movement of the Pacific tectonic plate over a hot spot, resulting in a series

of volcanoes with decreasing age from the northern part of the island to the southern part of the island (Spieth, 1982). This is the youngest island in the archipelago and consequently has the greatest potential of the current high islands for the effects of this conveyor-belt island formation to be demonstrated in a cladistic analysis. Wet forests ring these volcanoes and consequently are colonized by these flies. *Drosophila silvestris* populations have been examined in these wet forests for the past 20 years, and a great deal of information regarding the chromosomes, isozymes, and behavior of this species has been collected. The chromosomal and isozyme data (Carson, 1983c) are inconclusive as to the phylogeny of these populations. However, behavioral studies (Kaneshiro and Kurihara, 1981) clearly show a pattern of ancestral populations residing in the wet forests of the northern older volcanoes and more derived populations residing in the wet forests of the southern younger volcanoes. The mtDNA data set (see Figure 6.6) also detects this pattern, although not in the same degree of detail as the behavioral data. The lower level of resolution of the area relationships shown in Figure 6.6 under assumption 2 is the result of the more inclusive nature of this assumption (Page, 1990).

CONCLUSIONS

Molecular techniques can generate characters for use in biogeographic analysis of the Hawaiian Drosophilidae. Patterns can be detected at several biogeographic levels by using different taxonomic assemblages of these flies. Also, because different taxonomic levels are used to discover the patterns, the molecular approaches must change for the different levels. DNA sequences of slowly evolving mtDNA genes (rDNA) are used to examine the patterns of the origin of these Hawaiian fly lineages. The mtDNA data suggest that the Hawaiian lineages are monophyletic and that there is no clear continental subgenus *Drosophila* taxon that can be designated as the sole ancestor of the Hawaiian lineage. RFLP data from mtDNA is used to examine the species-level phylogeny of several closely related species groups and subgroups. This technique maximizes the amount of information for the effort used at this level.

A general area cladogram for six species groups (see Figure 6.5) indicates that there is a definite set of area relationships that are common to all six groups and subgroups of these flies. The uniformity of these area relationships may reflect the narrow ecological ranges (i.e., high-altitude wet forests) to which these flies are restricted. Also, once dispersal occurs,

it is also possible that the strong mating asymmetries and behavioral attributes observed in these flies (Spieth, 1982; Kaneshiro and Boake, 1987) contribute to the common pattern of area relationships from mtDNA cladograms. Mating asymmetries of these flies, discovered through experimental work (Giddings and Templeton, 1983; the Kaneshiro hypothesis, Kaneshiro, 1983; Kaneshiro and Giddings, 1987), imply strong behavioral isolation that might have a profound effect on the phylogenetic patterns observed for mtDNA. The Hawaiian archipelago is an ideal system for demonstrating this possibility. The sequence of formation of the Hawaiian archipelago would force colonization patterns to be common in groups that have the same dispersal capabilities such as these flies. If the mating asymmetries observed in the laboratory also affect these flies in nature, then an even stronger directional component would be enforced on the phylogenetic relationships of these flies.

RFLP and DNA sequence data are used to examine the possible area relationships within an island. Area relationships within the island of Hawai'i exist and, in general, follow a north-to-south direction. This result agrees with the temporal formation of the volcanoes and wet forests on the island of Hawai'i. The inability of the component analysis (see Figure 6.6) to diagnose the southernmost areas as distinct from each other is most likely due to the redundant distributions of the flies from these localities. The flow of genes among these populations is most likely responsible for this redundant distribution, although stochastic branching processes (Avice, 1986; DeSalle et al., 1986a) could also result in the types of distributions observed for *Drosophila silvestris* on the island of Hawai'i.

APPENDIX 6.1. Characters and Character States for mtDNA RFLPs for Inter-island Analysis

Species abbreviations are listed in Table 6.1. Area abbreviations are as follows: HK, Hawai'i (Kona side); HH, Hawai'i (Hilo side); EM, East Maui; WM, West Maui; MK, Moloka'i; OH, O'ahu; OG, outgroup. The data matrix for the beta *planitibia* study is taken from DeSalle and Giddings (1986), and restriction enzymes and restriction site maps can be obtained from that publication. All restriction sites listed in this matrix (A) are informative. Restriction enzyme abbreviations in the other five matrices are as follows: Xb, XbaI; Pv, PvuII; RI, EcoRI; RV, EcoRV; Cl, ClaI; HIII, HindIII; Nc, NcoI; Xh, XhoI; Bs, BstEII; Sc, SacI; Bc, BclI; Hp, HpaII. A "0" indicates the absence of a restriction site and a "1" indicates the presence. Some restriction sites listed in these five matrices are uninformative. Restriction site maps of each taxon are available from the author.

A. Picture-winged *planitibia* (beta)

| | | HH | HIII | BS | SC | NC | Xh | Xb | Cl | RV | Bc | Pv | RI |
|----|------|---|------|----|----|----|----|----|----|----|----|----|----|
| HH | silv | 1110001111000010111000010001010011101100111011001101100001001010100 | | | | | | | | | | | |
| HK | silv | 11100011110100111100001000101001101101101101101100001011110100 | | | | | | | | | | | |
| HK | hete | 1010001111010011000100001000010101110101011100001011010100 | | | | | | | | | | | |
| HH | hete | 101000111101001111000010001000010101110101011100001011010100 | | | | | | | | | | | |
| EM | plan | 11111000000111111100001100001010010100011111101001000110000 | | | | | | | | | | | |
| MK | diff | 0001110000110001110001001010100101100101110110011101100110100110000 | | | | | | | | | | | |
| OH | hemi | 0001010000101010001100000010001111011000010110000101100011010010000 | | | | | | | | | | | |
| OG | npct | 10010100001100001001101001001011000100000101000010010000001011 | | | | | | | | | | | |

B. *antopocerus*

| | | Xb | Pv | RI | RV | Cl | HIII |
|----|------|----------|-------|-----------|-------|----------|----------|
| HH | yoon | 10001010 | 01001 | 000011011 | 10000 | 11100010 | 00010111 |
| HH | cogn | 00110100 | 00111 | 100010011 | 10000 | 11000010 | 00010111 |
| HH | tany | 10001010 | 01001 | 000011011 | 10000 | 11100010 | 00010111 |
| EM | adun | 10001001 | 10000 | 100010111 | 10000 | 11000010 | 01000110 |
| MK | long | 10001001 | 10000 | 100100011 | 10000 | 11000010 | 00010110 |
| OG | arcu | 10001000 | 10000 | 100100011 | 00110 | 11000000 | 10000010 |

C. Picture-winged *hawaiiensis*

| | | HIII | Bs | Sc | NC | Xh | Xb | Cl | RV | Bc | Pv | RI |
|----|------|-------|----|---------|----|----|-----|------|-----|--------|------|-----------|
| HH | hawi | 01101 | 1 | 1000000 | 1 | 0 | 111 | 1100 | 101 | 110000 | 1000 | 100110111 |
| OG | musa | 11100 | 1 | 1110001 | 1 | 1 | 111 | 1110 | 100 | 110000 | 1100 | 101110111 |
| OH | grad | 11100 | 1 | 1110001 | 1 | 1 | 111 | 1110 | 100 | 100000 | 1101 | 110111111 |
| EM | rect | 11100 | 1 | 1100010 | 1 | 1 | 111 | 1110 | 110 | 101101 | 1000 | 100110111 |

(Continued on next page)

APPENDIX 6.1. (Continued)

D. Picture-winged *adiastola*

| | RI | Sc | Nc | Xh | Xb | CL | RV | PV | HIII |
|---------|---------|------------|------|------|----------|--------|---------|----------|--------------|
| EM adia | 1000101 | 0000110011 | 0100 | 0100 | 01011010 | 010101 | 0010010 | 00011000 | 110000010010 |
| HH seto | 1000101 | 0000111001 | 0100 | 1000 | 10100010 | 100001 | 0100000 | 00001101 | 01100100110 |
| OG clav | 0101000 | 1000001000 | 1000 | 0100 | 10100010 | 010101 | 0100000 | 01000010 | 101001000001 |
| MK cili | 1000101 | 0010010101 | 1000 | 0011 | 01011010 | 100001 | 0100000 | 01000010 | 101001000001 |
| MK spec | 0010111 | 0000111001 | 0011 | 0011 | 10100100 | 010101 | 0100000 | 00100100 | 011001100000 |
| EM peni | 1000101 | 0000010011 | 0100 | 0100 | 00011001 | 010101 | 0100000 | 00011000 | 011001100000 |

E. Picture-winged *affinidisjuncta*

| | Pv | RI | Xb | CL | RV | Sc | Xh | HIII | Bs | Nc |
|---------|-----------|--------------|---------|--------|----------------|-----------------|--------|-------------|--------|----|
| EM disj | 000001110 | 000011110111 | 1010001 | 010101 | 10000000000000 | 000010001000010 | 000110 | 01100011000 | 100000 | 10 |
| WM affi | 001000010 | 000011110111 | 1010001 | 100001 | 01000000000000 | 001000001000000 | 000110 | 01100011000 | 100000 | 10 |
| MK best | 000001110 | 100000000111 | 1010001 | 010101 | 10000000000000 | 001000001000000 | 010000 | 01100011000 | 010000 | 10 |
| OG grim | 100000000 | 001011100011 | 1010001 | 010101 | 01000000000000 | 000010001000001 | 010000 | 01100011000 | 010000 | 10 |

F. Picture-winged *planitibia* (alpha)

| | RI | Bc | CL | RV | HIII | Xh | Xb | Sc | Pv | Hp | Nc |
|---------|-----------------|--------------|----------|--------|---------------|----|----------|------------|--------------|----------------|------|
| EM cyrt | 01001000000001 | 100000000000 | 10000001 | 010000 | 1100001100000 | 01 | 01100010 | 0100000100 | 001100100000 | 0001001000000 | 0011 |
| EM mcph | 01001000000001 | 100000000000 | 10000001 | 100000 | 1100001100000 | 01 | 01100010 | 1000000000 | 001100100000 | 0001001000000 | 0011 |
| WM hana | 100000000000001 | 000011000000 | 10000001 | 100000 | 0101011100000 | 01 | 01100010 | 1000000000 | 001100100000 | 00001100000001 | 0011 |
| MK npki | 010010000000001 | 010000010000 | 00011000 | 000110 | 0101011100000 | 01 | 01100010 | 0010000101 | 001100100000 | 01000000000001 | 0011 |
| EM obsc | 010010000000001 | 100000000000 | 10000001 | 100000 | 0101011100000 | 01 | 01100010 | 1000000000 | 001100100000 | 01000000000001 | 0011 |
| OH nigh | 01000010000101 | 000100000100 | 00100100 | 010000 | 010001111010 | 10 | 01100010 | 000010101 | 00101110000 | 0010000001011 | 1000 |
| OH oahu | 10000000101001 | 000000000101 | 10000001 | 010000 | 010001111010 | 10 | 01010001 | 000010101 | 01000011000 | 10000000000000 | 0100 |
| MK npct | 0010011000111 | 000011000000 | 10000001 | 001001 | 0101011100000 | 10 | 10001010 | 000010111 | 01000010010 | 0000000110101 | 1000 |
| OG pict | 0011000010001 | 000000000010 | 10000001 | 010000 | 001011000101 | 10 | 01010110 | 100000000 | 100000000101 | 10000000000000 | 0100 |

APPENDIX 6.2. Characters of the Six Selected Species Groups Listed in Table 6.1 Used in the Construction of the General Area Cladogram

An, *antopocerus*; adi, *adiastola*; bet, beta *planitibia*; Alp, alpha *planitibia*; Aff, *affinidisjuncta*; Haw, *hawaiiensis*; ?, missing data.

| Area | An | Adi | Bet | Alp | Aff | Haw |
|-------------------|-----|-----|-----|------|-----|-----|
| Ancestor | 000 | 000 | 000 | 0000 | 00 | 00 |
| O'ahu | 001 | ??? | 001 | 0001 | ?? | 01 |
| Moloka'i | 011 | 011 | 001 | 0011 | 01 | ?? |
| West Maui | ??? | ??? | ??? | 0111 | 11 | ?? |
| East Maui 1 | 111 | 111 | 011 | 1111 | 11 | 11 |
| East Maui 2 | ??? | ??? | ??? | 1111 | ?? | ?? |
| Hawai'i Kona side | ??? | ??? | 111 | ???? | ?? | ?? |
| Hawai'i Hilo side | 111 | 111 | 111 | ???? | ?? | 11 |

APPENDIX 6.3. Characters and States for the Intra-island Study

Abbr, abbreviations used in Figure 6.6; four-base cutter data from DeSalle and Templeton (1992); six-base cutter data from DeSalle et al. (1986b); Seq, two characters from the DNA sequencing study (DeSalle and Templeton, 1992).

| Area | Abbr | Characters | | |
|-------------|------|-------------------------|---------------|-----|
| | | 4-base cutter | 6-base cutter | Seq |
| 'Ola'a 1 | H4-1 | 11000101100101010110101 | 01000000 | 11 |
| 'Ola'a 2 | H4-2 | 11000101101101101000101 | 01100110 | 11 |
| Kilauea | H5 | 11100101100101101000101 | 01101110 | 11 |
| Pi'ihonua 1 | H3-1 | 00101100100001000000001 | 01111010 | 11 |
| Pi'ihonua 2 | H3-2 | 10000011100001000010001 | 11000100 | 11 |
| Pi'ihonua 3 | H3-3 | 10001100100001000000001 | 01001111 | 11 |
| Pi'ihonua 4 | H3-4 | 10000101101001101000101 | 01100110 | 11 |
| Maulua | H2 | 10011110010001010111010 | 00001100 | 11 |
| Kohala | H1 | 00011000010010000001010 | 01100110 | 00 |
| Kona | K | 10001010000010000011000 | 10010101 | 00 |

7 Evolution of *Sarona* (Heteroptera, Miridae)

Speciation on Geographic and Ecological Islands

ADAM ASQUITH

Very often, however, we find species, extremely closely allied species, occurring habitually in the same locality and not geographically isolated.

—R. C. L. PERKINS, 1913

In most models of allopatric speciation, a geographic barrier to gene flow is required for, or greatly facilitates, speciation (Mayr, 1963; Carson and Templeton, 1984; Carson, 1987a; Barton, 1988). Nowhere is the pattern of gene flow barriers so conspicuous, discrete, and repeated than in island archipelagoes. The conventional model of allopatric speciation in an archipelago with an ontogeny, such as the Hawaiian Islands, is that when a new island is formed, it is colonized by founders from a species on the nearest island (Zimmerman, 1948; Carson, 1987b; see also Carson and Clague, this volume, Chapter 2). Speciation ensues among these isolated founders, and the process is repeated when the next island is formed. This process produces a pattern of single-island endemics in which the sister species to any taxon occurs on the most proximate, older island.

This is the most simplistic model of speciation in the Hawaiian Islands and probably explains the evolution of many groups of insects, such as the orthopteran genus *Banza* (Tettigoniidae) (J. Strazanac, unpubl.) and the heteropteran genus *Kamehameha* (Miridae) (A. Asquith, unpubl.). This pattern can be complicated by back-dispersal to older islands (Carson, 1987b; see also Lowrey, this volume, Chapter 11) or allopatric speciation within islands, such as among volcanoes, isolation in

kipuka (Zimmerman, 1948), restriction to ecological communities (Howarth, 1991), or social or sexual selection (Kaneshiro, 1983; Carson, 1986; Otte, 1989).

Whether they represent inter- or intra-island speciation, all the processes mentioned above involve some degree of geographic isolation. Theoretically, however, complete isolation is not necessary for speciation (Endler, 1977; Wright, 1982). Ecological factors such as microhabitat specialization (Kaneshiro et al., 1973) or phenological partitioning (Wood, 1980; Wood and Guttman, 1982) can prove to be extrinsic barriers sufficient to precipitate divergence. Although the ecological diversification of many Hawaiian insect groups is often touted as exemplifying insular evolution, rarely is speciation argued as being directly linked to these ecological radiations. Sympatric speciation by host plant or habitat shifts has been suggested for some Hawaiian *Drosophila* species (Kaneshiro et al., 1973; Carson and Ohta, 1981), but putative sister species typically have similar if not identical ecological traits (Carson and Kaneshiro, 1976).

The potential for sympatric, ecological barriers is perhaps greatest among phytophagous insects that are host plant-specific (Bush, 1974, 1975; Bush and Diehl, 1982; Bush and Howard, 1986). Many groups of phytophagous Hawaiian insects have been noted for their radiations onto different host plants (Usinger, 1942; Zimmerman, 1948; Gressitt, 1978), but species relationships in most groups are poorly understood at best. In this chapter, I examine the evolution of the endemic phytophagous plant bug genus *Sarona*. With only one exception, *Sarona* species are single-island endemics, and each species feeds, breeds, and develops on a single species of host plant. Using cladistic analysis for the identification of sister taxa, I attempt to elucidate the relative roles of geographic versus ecological barriers in speciation in this genus. For the purposes of zoological nomenclature none of the names in *Sarona* mentioned in this chapter is for the permanent scientific record.

ORIGINS

The orthotyline plant bug genus *Sarona*, with 40 known species (Table 7.1), is endemic to the Hawaiian Islands. The North American genera *Slaterocoris* and *Scalponotatus* together have been identified as the sister group to *Sarona* (Asquith, 1994b). The outgroup to these three genera is unknown but is likely another North or Central American

TABLE 7.1. Island Distributions and Host Plants of *Sarona* Species

| Species | Island ^a | Host Plant ^b | Family |
|------------------------|---------------------|---|---------------|
| <i>S. adonias</i> | MoMLH | <i>Metrosideros polymorpha</i> Gaud. | Myrtaceae |
| <i>S. akoko</i> | K | <i>Chamaesyce</i> | Euphorbiaceae |
| <i>S. alani</i> | H | <i>Melicope</i> | Rutaceae |
| <i>S. annae</i> | K | <i>Zanthoxylum</i> | Rutaceae |
| <i>S. antennata</i> | Mo | <i>Pipturus</i> | Urticaceae |
| <i>S. aula</i> | L | <i>Ilex anomala</i> Hook. & Arnott | Aquifoliaceae |
| <i>S. azophila</i> | L | <i>Nestegis sandwicensis</i> (A. Gray) Degener et al. | Oleaceae |
| <i>S. beardsleyi</i> | M | <i>Nestegis sandwicensis</i> | Oleaceae |
| <i>S. dakine</i> | M | <i>Melicope</i> ? | Rutaceae |
| <i>S. flavidorsum</i> | H | <i>Korthalsella</i> | Viscaceae |
| <i>S. gagnei</i> | O | <i>Korthalsella complanata</i> (Tiegh.) Engl. | Viscaceae |
| <i>S. haleakala</i> | EM | <i>Dubautia menziesii</i> (A. Gray) D. Keck | Asteraceae |
| <i>S. hamakua</i> | H | <i>Myrsine</i> | Myrsinaceae |
| <i>S. hie</i> | O | <i>Melicope</i> ? | Rutaceae |
| <i>S. hiiaka</i> | K | <i>Melicope clusiifolia</i> (A. Gray) T. Hartley & B. Stone | Rutaceae |
| <i>S. iki</i> | H | Unknown | |
| <i>S. kaala</i> | O | <i>Broussaisia arguta</i> Gaud. | Hydrangeaceae |
| <i>S. kanaka</i> | EM | <i>Cheirodendron</i> ? | Araliaceae |
| <i>S. kane</i> | EM | <i>Myrsine</i> | Myrsinaceae |
| <i>S. kau</i> | H | <i>Dubautia</i> | Asteraceae |
| <i>S. kohana</i> | O | Unknown | |
| <i>S. kuaana</i> | O | <i>Metrosideros</i> ? | Myrtaceae |
| <i>S. kukona</i> | K | <i>Melicope barbigera</i> A. Gray | Rutaceae |
| <i>S. laka</i> | K | <i>Claoxylon sandwicense</i> Müll. Arg. | Euphorbiaceae |
| <i>S. lanaiensis</i> | L | <i>Pipturus</i> | Urticaceae |
| <i>S. lissochorium</i> | O | <i>Broussaisia</i> ? | Hydrangeaceae |
| <i>S. makua</i> | K | Unknown | |
| <i>S. mamaki</i> | H | <i>Pipturus</i> | Urticaceae |
| <i>S. maui</i> | EM | <i>Pipturus</i> | Urticaceae |
| <i>S. mokiha</i> | K | <i>Melicope anisata</i> (H. Mann) T. Hartley & B. Stone | Rutaceae |
| <i>S. myoporicola</i> | H | <i>Myoporum sandwicense</i> A. Gray | Myoporaceae |
| <i>S. oahuensis</i> | O | <i>Coprosma</i> ? | Rubiaceae |

(Continued)

TABLE 7.1. (Continued)

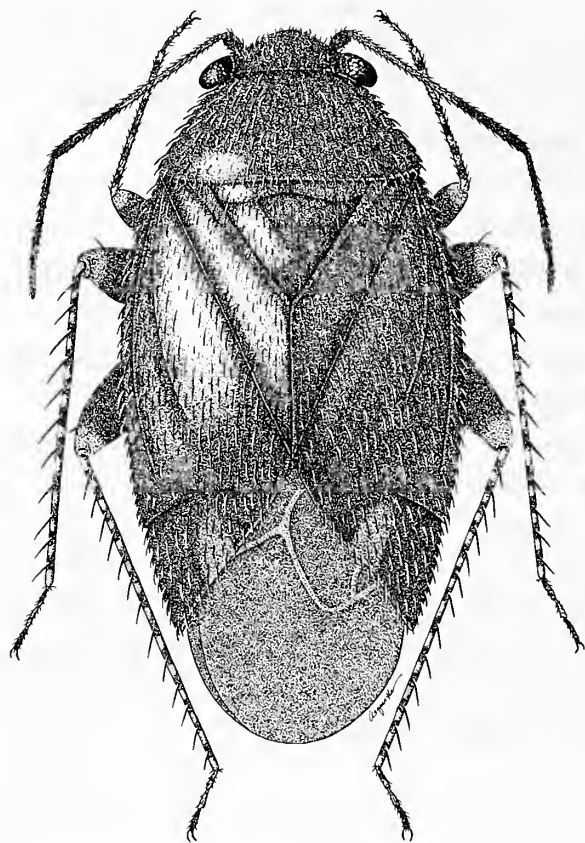
| Species | Island ^a | Host Plant ^b | Family |
|------------------------|---------------------|---|----------------|
| <i>S. oloa</i> | O | <i>Neraudia</i> <i>melastomifolia</i> Gaud. | Urticaceae |
| <i>S. palolo</i> | O | Unknown | |
| <i>S. pittospori</i> | H | <i>Pittosporum</i> | Pittosporaceae |
| <i>S. pookoi</i> | Mo | Unknown | |
| <i>S. pusilla</i> | M | <i>Pipturus</i> | Urticaceae |
| <i>S. saltator</i> | K | <i>Melicope clusiifolia</i> | Rutaceae |
| <i>S. usingeri</i> | O | <i>Claoxylon</i> <i>sandwicense</i> ? | Euphorbiaceae |
| <i>S. xanthostelma</i> | O | Unknown | |

^aK, Kaua'i; O, O'ahu; Mo, Moloka'i; M, Maui; EM, East Maui; L, Lana'i; H, Hawai'i.
^bConfirmation of host plants was based on the collection of more than six adults (in some cases, many more) or the presence of immatures. ?, a questionable or unconfirmed host (i.e., fewer than six adults have been collected from the plant).

taxon, as there are no Asian or Indo-Pacific genera with any affinities to this group (Asquith, 1994b). Making the assumption that continent-to-island colonization is more likely than the reverse (Ward and Brookfield, 1992; Asquith, 1994a), then the ancestor of *Sarona* colonized the Hawaiian Islands from western North America. This places *Sarona* in a minority group of Hawaiian insects believed to be derived from North America, including the plagithmysine Cerambycidae (Gressitt, 1978), the oecanthine and trigonidiine crickets (Otte, 1989), and the metrargine Lygaeidae (Asquith, 1994a).

The identification of the sister taxon of *Sarona* gives us a base from which to make a comparative analysis of insular versus continental evolution. For example, because of the allopatric barriers inherent in archipelagoes, it is sometimes argued that they facilitate and increase the rate of speciation (Mayr, 1942; Williamson, 1981), with the radiation of the Hawaiian Drosophilidae held as an example. The sister group to *Sarona* (*Slaterocoris* and *Scalponotatus*) contains approximately 50 species; if sister taxa are of equal geologic age (Hennig, 1966), then the archipelago endemic *Sarona*, with 40 species, has not undergone a greater speciation rate than its continental sister taxon. However, extinction rates on islands are probably greater than in continental areas (MacArthur and Wilson, 1967), and additional species of *Sarona* were probably present

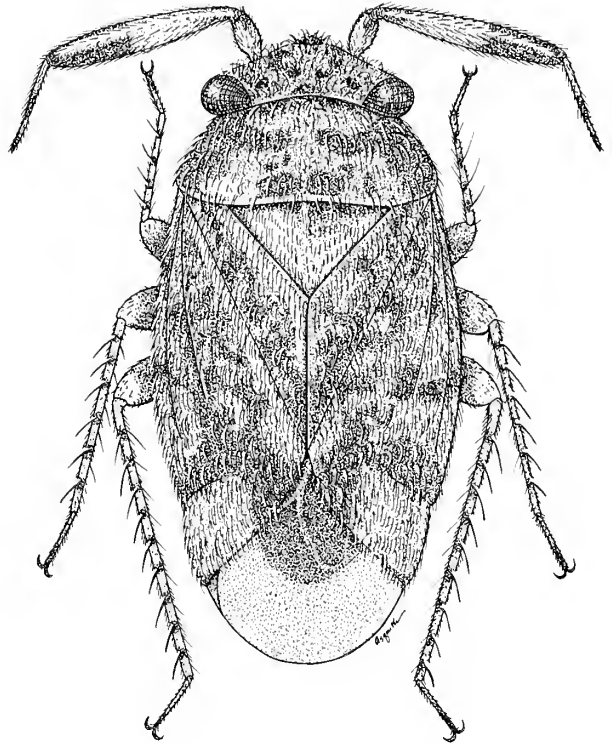
FIGURE 7.1. *Sarona saltator*.
Dorsal habitus.



on older, once-emergent islands, so that cumulatively, *Sarona* may actually have had more species than the extant taxa alone indicate.

In contrast to groups such as the Drosophilidae (Hardy, 1965), Cosmopterigidae (Zimmerman, 1978), and the plagithmysine Cerambycidae (Gressitt, 1978), which have undergone spectacular morphological radiations in the Hawaiian Islands, the evolution of *Sarona* has been morphologically conservative (Figures 7.1 and 7.2, illustrating the extremes of body form), with most interspecific variation occurring in male genitalic structures. Also, the genitalic differences among species of *Slaterocoris* and *Scalponotatus* involve the same structures and are of the same general magnitude as those seen in *Sarona*. *Sarona* has apparently undergone an extensive ecological radiation, however. Its continental sister taxon is known to breed on 13 genera of plants in four families, predominantly in the Asteraceae (Kelton, 1968, 1969). Species of *Sarona*, however, are known from 17 genera of plants in 14 families (Table 7.1). Although it would be more convincing to compare the radiation of *Sarona* with the sister group consisting of *Sarona*, *Scalponotatus*, and *Slaterocoris*, this relationship is not known. Most other genera of North

FIGURE 7.2. *Saronia oloa*. Dorsal habitus.



American orthotyline, however, typically have taxonomically restricted host plant associations of one to four families, certainly much narrower than those displayed by *Saronia*.

Thus, the only distinct difference between the archipelago and continental radiations in this group is the ecological colonization of a large number of new host plant families by *Saronia*. This is in contrast to Gagné's (1983) contention that the diversity of host plant families that *Saronia* uses is a consequence of its having evolved from a polyphagous ancestor.

PHYLOGENETIC ANALYSIS

The genera *Scalponotatus* and *Slaterocoris* were used as a composite outgroup to polarize characters analyzed with the phylogenetics program HENNIG86 (Farris, 1988). Most of the character information was coded in a two-state format (Appendixes 7.1 and 7.2). Most multistate characters, with the exception of characters 4 and 20, were linearly ordered. Other multistate characters were multiple-branched; because HENNIG86 does not support complex branching characters, a form of additive binary coding was used (e.g., characters 4 and 5). The ordering of character states was derived from hypothesized transformation series based on

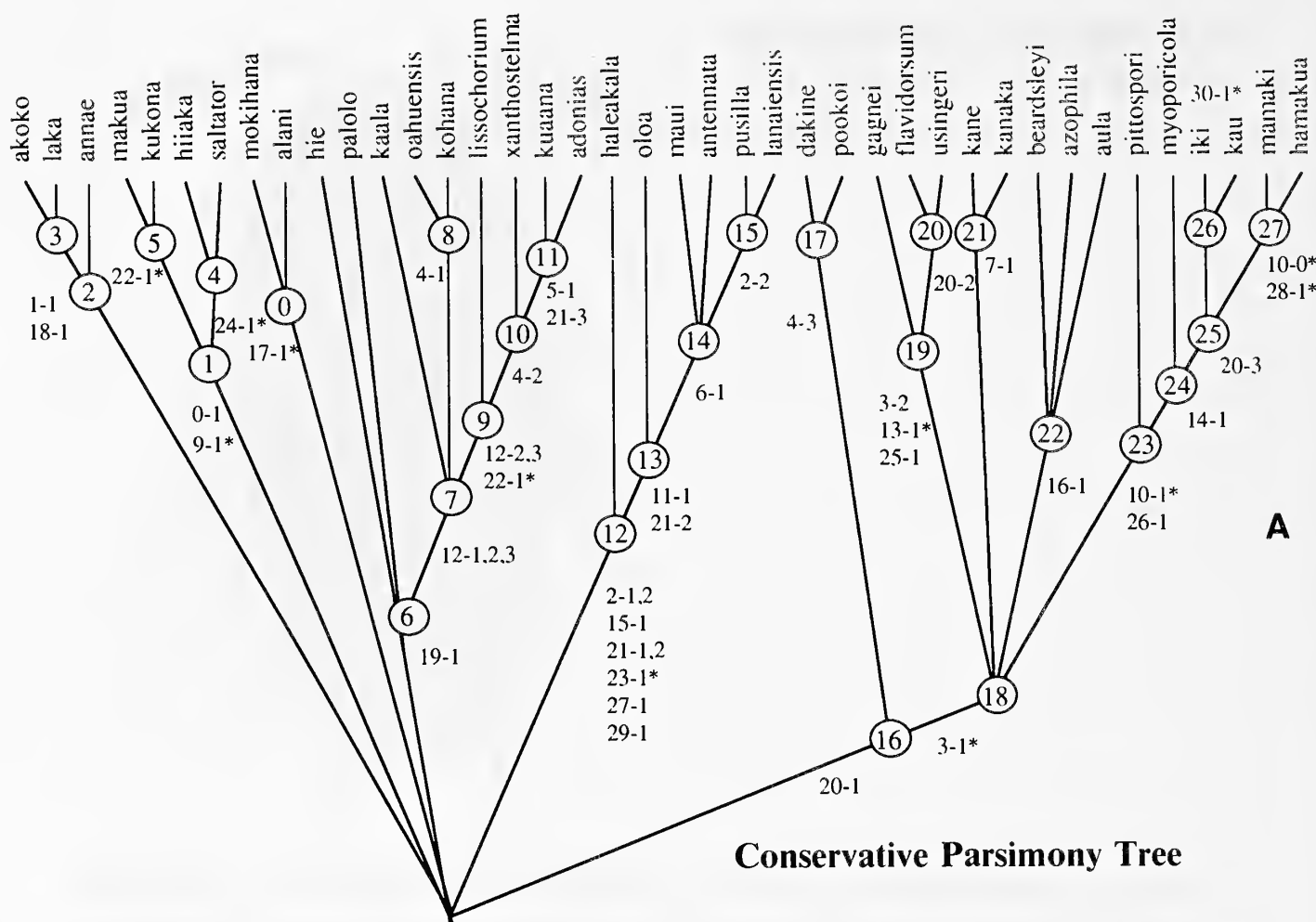


FIGURE 7.3. Three variations (A–C) in tree topology from 56 equally parsimonious trees of *Sarona* species, based on analysis of a 31-character data set. Numbers in small type are characters followed by character states. An asterisk indicates homoplasy or reversal. Numbers in circles are node designations. The most conservative variation is (A), because *S. mokihana* and *S. alani* arise from the basal polytomy. (Continued on next page)

morphoclines. Analyses using the mh* and bb* options (Fitzugh, 1989) produced 910 trees, all with lengths of 62 and consistency indexes (CI) of 0.64. Successive weighting procedures of the initial 910 trees reduced the number of trees to 56. This procedure was applied to reduce the number of trees to be examined and to choose those trees with the most consistent characters (Carpenter, 1988).

All differences among the 56 trees involved the relationships of *Sarona alani*, *S. mokihana*, and *S. annae* to nodes 1 and 4 (Figure 7.3). Four of the 56 trees united *S. annae* with those taxa at node 12, and *S. laka* and *S. akoko* were placed at node 1 (Figure 7.3C). Fifty-two of the 56 trees united *S. annae* with *S. akoko* and *S. laka* (node 2) based on two synapomorphies (characters 1 and 18), and I interpret these three species as comprising a monophyletic group (Figure 7.3A). The trees that recognized node 2 in Figure 7.3A also interpreted character 9 (digitiform basal

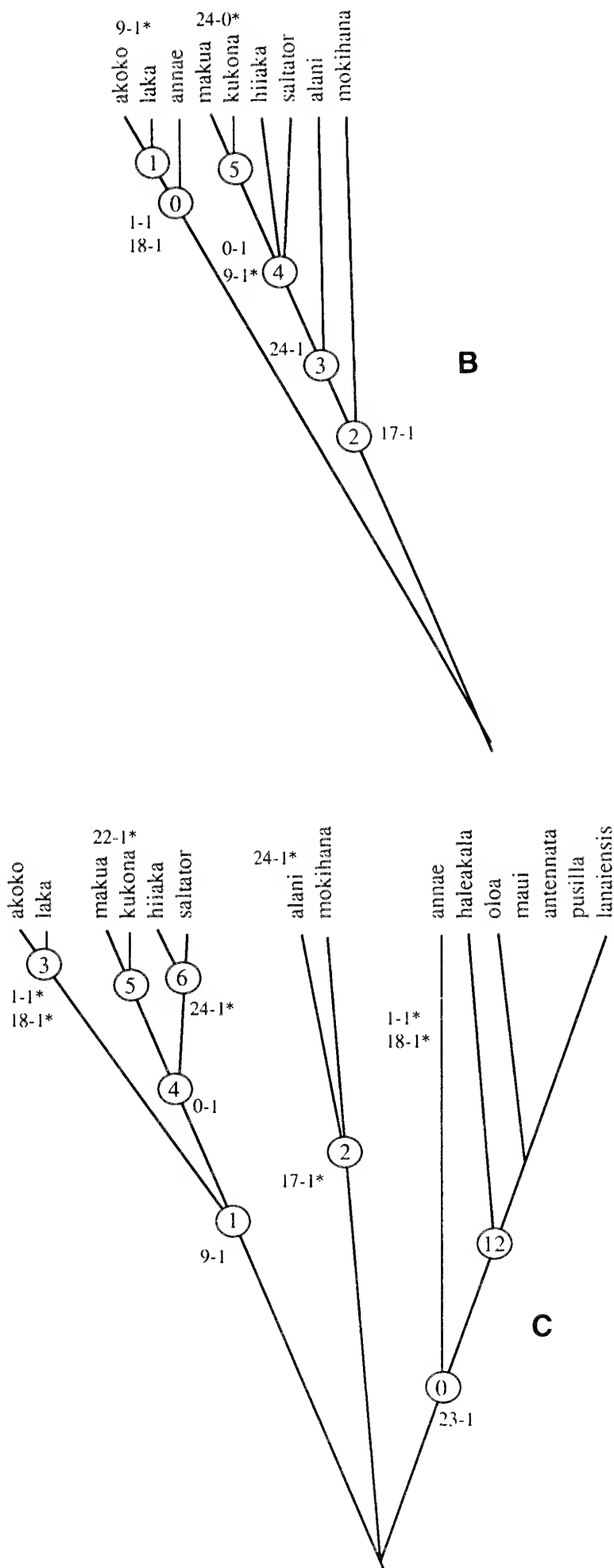


FIGURE 7.3. (Continued)

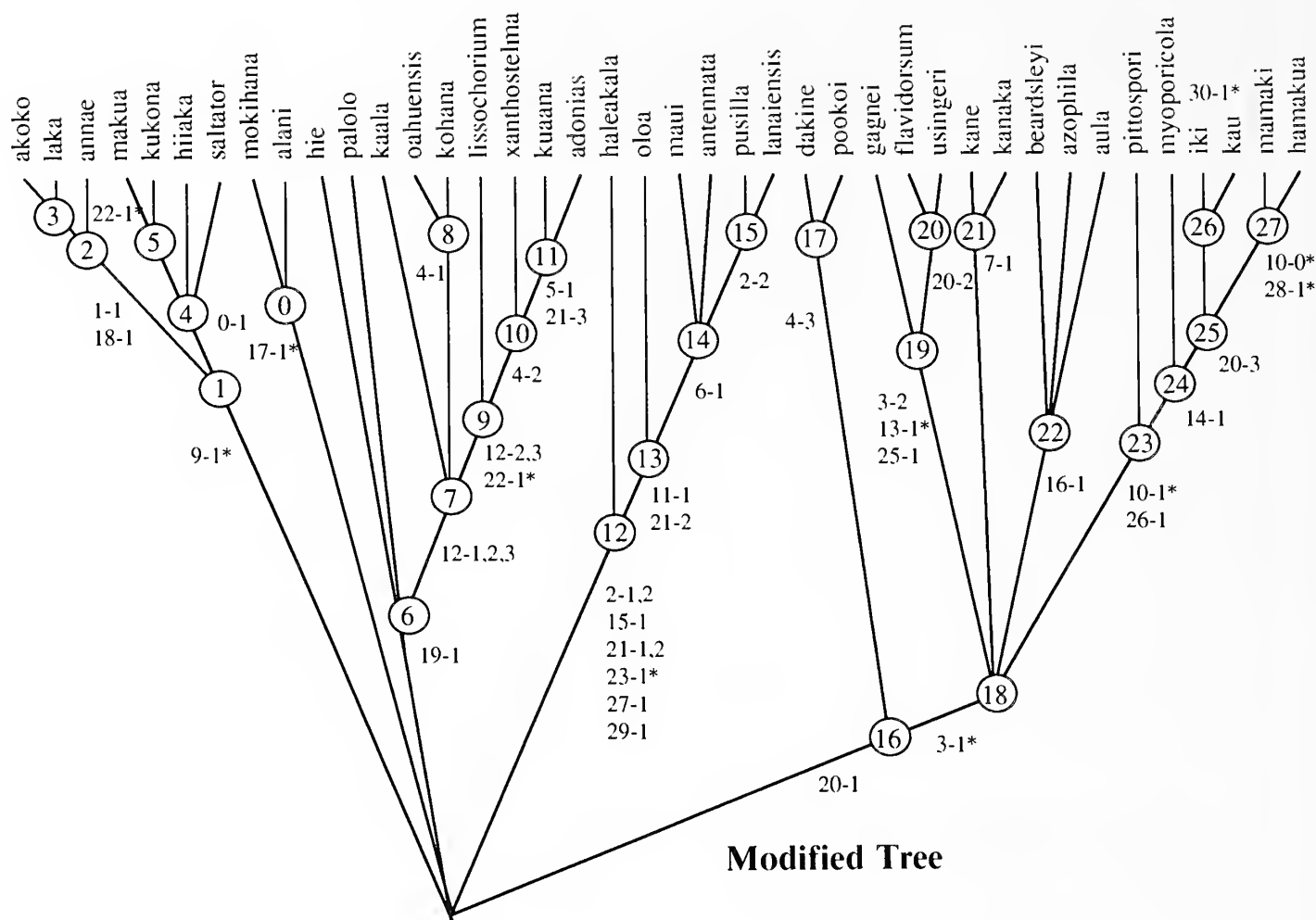


FIGURE 7.4. Modified cladogram of *Sarona* species based on analysis of 31-character data set. Numbers in small type are characters followed by character states. An asterisk indicates homoplasy or reversal. Numbers in circles are node designations. This cladogram is used in all further hypotheses of evolutionary patterns in *Sarona*.

angle of the left paramere) as arising twice, once in the ancestor of *S. akoko* and *S. laka*, and again in the ancestor of *S. hiiaka*, *S. saltator*, *S. makua*, and *S. kukona*. I take the view of Wheeler (1986), that the blind application of parsimony without reevaluating the validity of the characters is credulous. Character 9 is not variable in the outgroup, it would not be affected by an ecological shift, and it is interpreted as a synapomorphy for *S. akoko*, *S. laka*, and the taxa at node 1 in four of the trees (Figure 7.3C). I argue that it is more logical to interpret this character as a synapomorphy for all these species (node 1 in Figure 7.4; hereafter called the *Kaua'i* group), with a character state reversal in *S. annae* (Figure 7.4). This hypothesis increases the total length of the tree by one step and reduces the CI by 0.01, but it is the topology I will use to discuss evolutionary patterns.

The analysis also either united *Sarona alani* and *S. mokihana* as a monophyletic group arising from the basal polytomy or placed them at

node 2 (Figure 7.3B). Both these species retain the plesiomorphic condition of a medially positioned basal arm of the right paramere. Although these two taxa lack the synapomorphy (character 9) uniting all other taxa of the *Kaua'i* group, they both share other synapomorphies with some species in this clade. *Sarona mokihana* has a narrowly acuminate ventral margin of the genital capsule (character 17), which also occurs in *S. saltator* and *S. kukona*. *Sarona alani* shares modified setae around the base of the ovipositor (character 24) with *S. hiiaka* and *S. saltator* but also has a digitiform apex of the spicula flange, which may be homologous with the condition in the *adonias* group (character 19). The rest of the spicula is highly modified, however, making it difficult to use this character to place *S. alani* in any species group.

Let it suffice to say that the exact relationships of *Sarona alani* and *S. mokihana* are equivocal and I conservatively treat them as basally unresolved (Figures 7.3A and 7.4), but their affinities certainly lie with the *Kaua'i* group.

Apart from the ambiguity of *Sarona alani* and *S. mokihana*, the pattern of the cladogram is such that species groups are well defined, but there is little resolution of group relationships (Figure 7.4). Node 16 is supported by a reduced spicula (20–1), but spiculae are not homogeneous within this clade, and the reduced state in some species (i.e., *S. dakine* and *S. pookoi*) may be homoplasious. A similar problem occurs with the cylindrical right paramere (3–1) supporting node 18. The reduced condition (3–2) was coded as a transition but may actually be an independently derived condition. If this is true, the *flavidorsum* group (node 19) would not be united with the rest of the taxa at node 18.

The analysis did, however, identify at least three large, distinct species groups (nodes 6, 12, and 23). Node 6, referred to as the *O'ahu* group, is supported by the digitiform apex of the spicular flange (19–1). Node 9 (the *adonias* group) is supported by the presence of two tergal processes, with the primary one enlarged (12–2). The serrate apex of the spicula (22–1) also represents a synapomorphy for this group, but the condition also occurs in *Sarona kohana* and *S. makua*. This condition is actually widespread in other orthotyline genera, but it is here treated as a synapomorphy because it occurs in some but not all species used in the outgroup.

Sarona lissochorium is clearly united with *S. xanthostelma*, *S. kuaana*, and *S. adonias* by the tergal processes (12–2) but lacks the distinct C-shaped right paramere (4–2) of the other three species. This indicates that the C- and L-shaped parameres are derived from the ancestral

cylindrical form (22–0), and this derived state has evolved independently in *Sarona* at least three times (*adonias* group, *S. annae*, and *S. dakine*) and possibly four (*S. oahuensis* and *S. kohana*).

Node 12 (*antennata* group) represents the best-defined clade in the genus. It is supported by five unique synapomorphies. Sericeous setae (23–1) are also found in some but not all species in the outgroup, and the presence of the setae is treated as derived in *Sarona*. *Sarona annae*, in the *Kaua'i* group, also has sericeous setae and superficially strongly resembles other members of the *antennata* group. *Sarona annae* lacks all other synapomorphies of the *antennata* group, however, and I therefore interpret the sericeous setae of *S. annae* as of independent origin. Relationships within this clade are fairly well resolved and supported by strong synapomorphies.

Node 23 (the *myoporicola* group) is identified by having conspicuously banded or bicolored femora (26–1). Other species of *Sarona* sometimes have indistinct bands on the posterior femora but never wide, distinct bands on all femora as seen in the *myoporicola* group. All species except *S. pittospori* are also united by having the tergal process modified as two short teeth (14–1). The acuminate spicula flange (20–3) further identifies *S. kau*, *S. iki*, *S. mamaki*, and *S. hamakua* as monophyletic.

All other clades represent smaller species groups supported by unequivocal synapomorphies.

BIOGEOGRAPHY

In the cladogram (Figure 7.4), most species groups are essentially polytomous, making it difficult to polarize colonizations among islands by species groups (Figure 7.5). Even the basal taxa, *Sarona mokiha* and *S. alani*, are enigmatic in that both are presumably plesiomorphic, providing the potential to polarize inter-island colonizations, but they are found at different ends of the archipelago.

Two lines of evidence, however, argue for the plesiomorphic nature of *Kaua'i* taxa. First, cladistics argues only that derived sister taxa will share synapomorphic character states and that characters should change congruently (Hennig, 1966; Mickevich, 1978). The corollary of this is that character states of geologically older taxa should be plesiomorphic (Hennig's geologic character precedence). Indeed, only *Kaua'i* species display character states that are clearly unchanged from the condition observed in the outgroup. *Sarona makua* is the only species to have

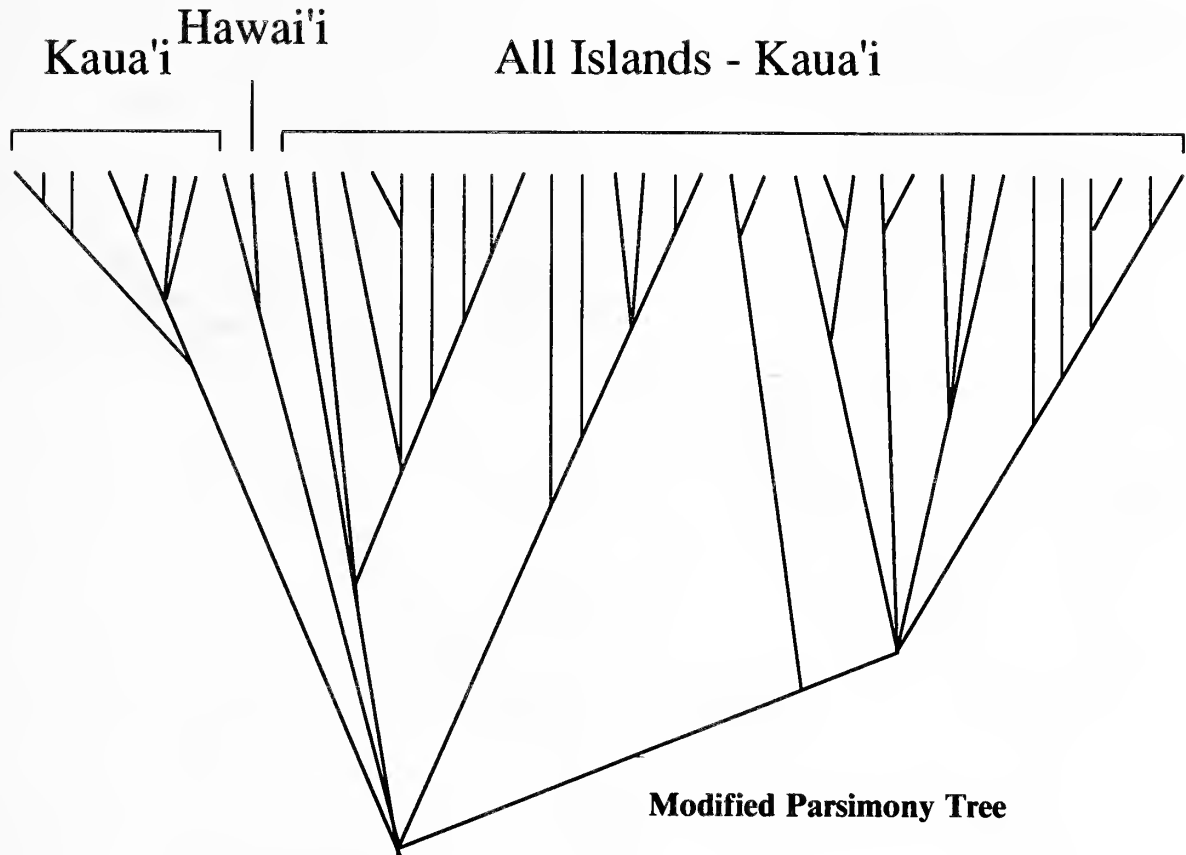


FIGURE 7.5. Island distribution of species of *Sarona* in modified cladogram (Figure 7.4).

retained the primitive condition of the apicomedial flange on the left paramere (character 8) (although this is treated as a reversal in the analysis). *Sarona hiiaka* and *S. mokiha* have the spiculae weakly bent or recurved, which is also a plesiomorphic state in *Sarona*, although not used in the analysis.

Second, geologically older taxa may also display more autapomorphies than younger taxa. This condition could arise if character evolution is not strictly a consequence of speciation but occurs randomly at a more or less constant rate, such as nucleotide or amino acid replacements (Wilson et al., 1987). Also, anagenetic change, even in morphological characters, may be associated with environmental stability (Coope, 1979; Futuyma, 1989) such as that found in Hawaiian wet forests. If characters respond to selection, however, geologically older taxa that have adapted to environmental changes would still have acquired autapomorphies.

Even if autapomorphies arise only with speciation, in an archipelago, where older islands and their associated fauna eventually disappear, we would observe a pattern of characters changing from autapomorphy to synapomorphy to autapomorphy again. In Figure 7.6, for example, let

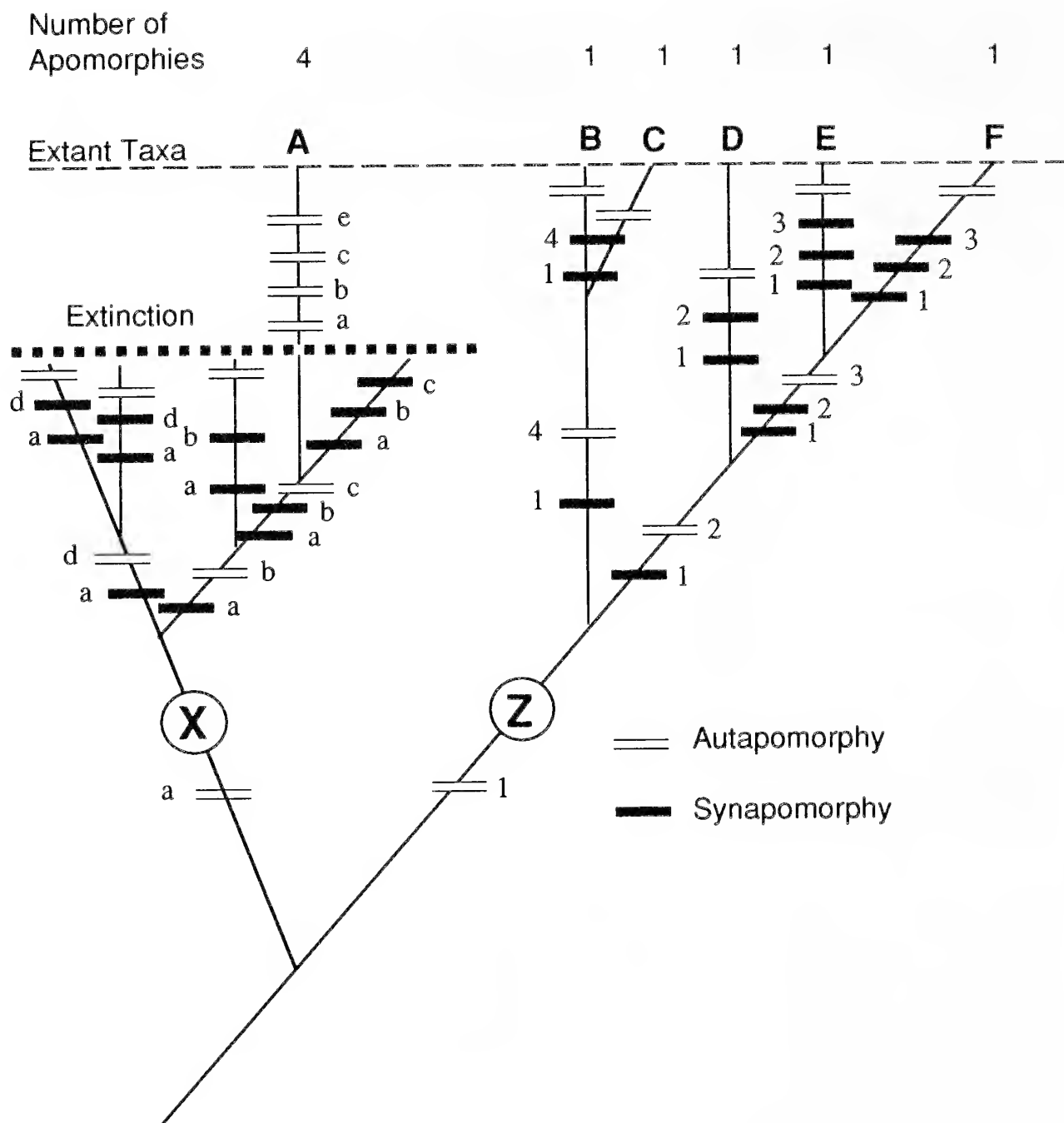


FIGURE 7.6. Hypothetical cladogram of an Hawaiian Island species group, illustrating how characters change from autapomorphies to synapomorphies and back to autapomorphies in species whose sister taxa are extinct. Species A represents a relictual taxon on an older island such as Kaua'i, whereas species B to F represent more recent cladogenesis on a younger island such as Hawai'i.

us assume that usually one unique autapomorphy arises in each descendent species. What was an autapomorphy in an ancestral species, however, becomes a shared synapomorphy in the descendants. In clade Z (on a young island), with descendent taxa from all speciation events reaching the present time, the only autapomorphies that have not become synapomorphies are those that arose in the most recent speciation event, one in each extant species. In clade X (on an older island), however, charac-

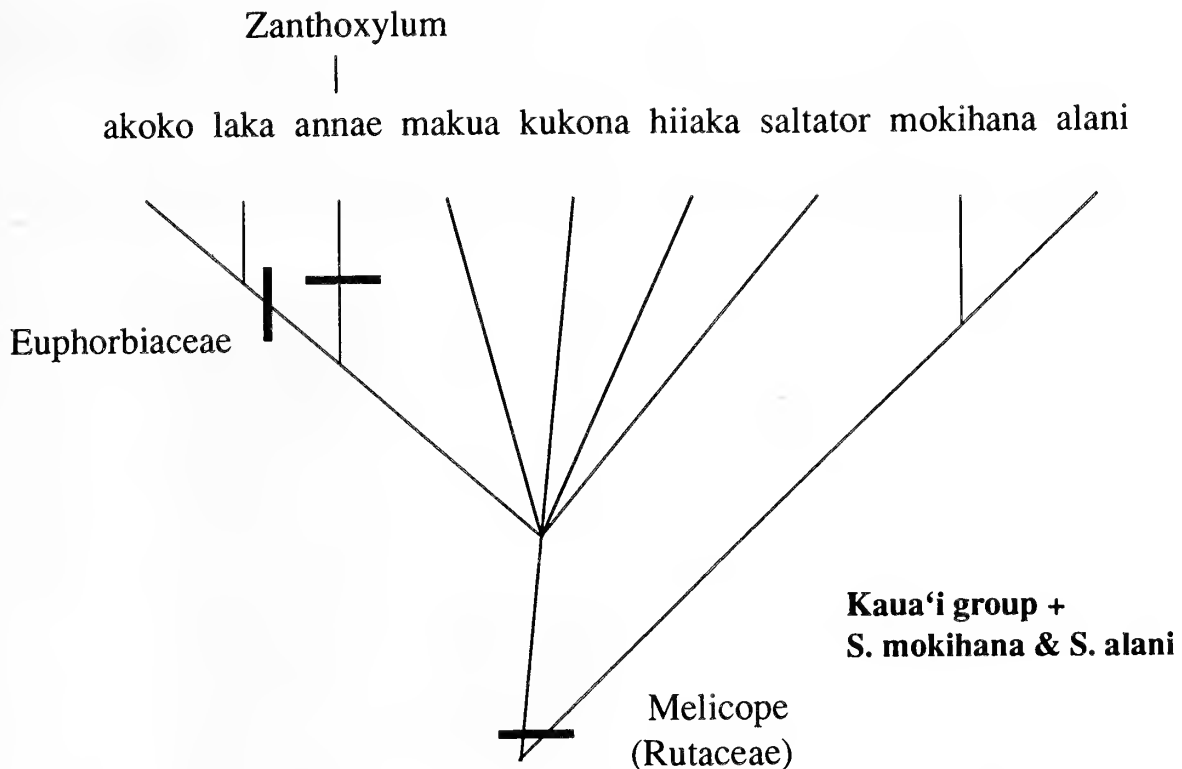


FIGURE 7.7. Relationships and host plant associations in the *Kaua'i* species group.

ters a to c arise as autapomorphies, become synapomorphies after speciation events, and then, with the extinction of most taxa possessing these characters, are perceived as autapomorphies in the extant species A. In applying this hypothesis to *Sarona*, the Hawai'i Island species *S. adonias*, *S. flavidorsum*, and *S. alani* all share significant synapomorphies with their sister taxa on older islands, which presumably arose as autapomorphies in their respective common ancestors (Figures 7.7 to 7.9). If these three Hawai'i taxa persist until the extinction of their sister taxa and do not undergo cladogenesis, what were once synapomorphies would then be perceived as autapomorphies (see Figure 7.6). The same result could be achieved by extinction of all sister taxa on the same island. Under this scenario, the observation that Kaua'i species and *S. alani* have four times the average number of autapomorphies compared with species on other islands (Figure 7.10) argues for their more primitive status.

With the exception of *Sarona mokihana*, the sister taxa of all Kaua'i species also occur on Kaua'i. Considering the plesiomorphies discussed above and the synapomorphies shared by *S. mokihana* with other Kaua'i species and assuming the presence of *S. alani* on Hawai'i to be derived, then all Kaua'i species appear to have evolved on Kaua'i or a pre-Kaua'i island, and there is no evidence suggesting origins from the younger

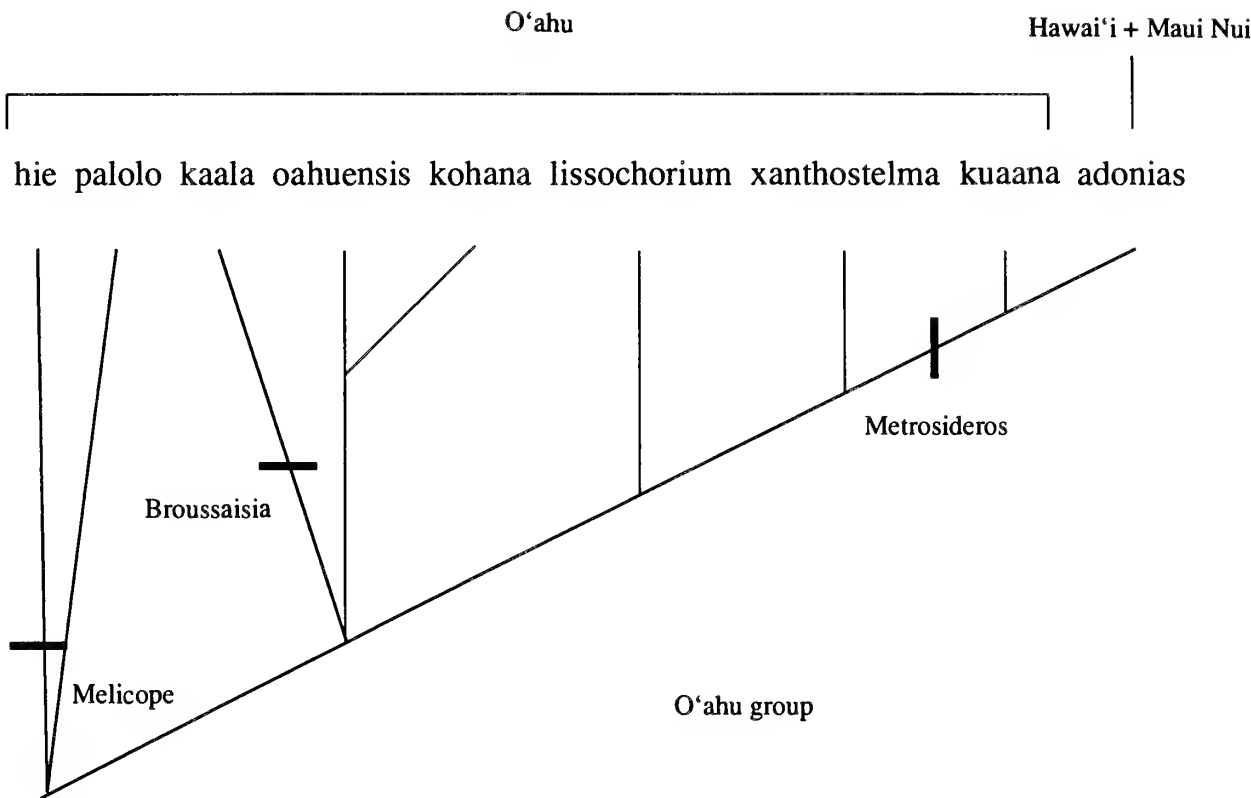


FIGURE 7.8. Relationships, distributions, and host plant associations in the *O'ahu* species group.

islands. Furthermore, if we consider the island of Hawai'i as an example, where there are taxa from three different species groups (see below), then there is no a priori reason to expect all Kaua'i species to form a strong monophyletic group. Rather, just as on younger islands such as Hawai'i, it is likely that *Sarona* reached Kaua'i from older islands multiple times.

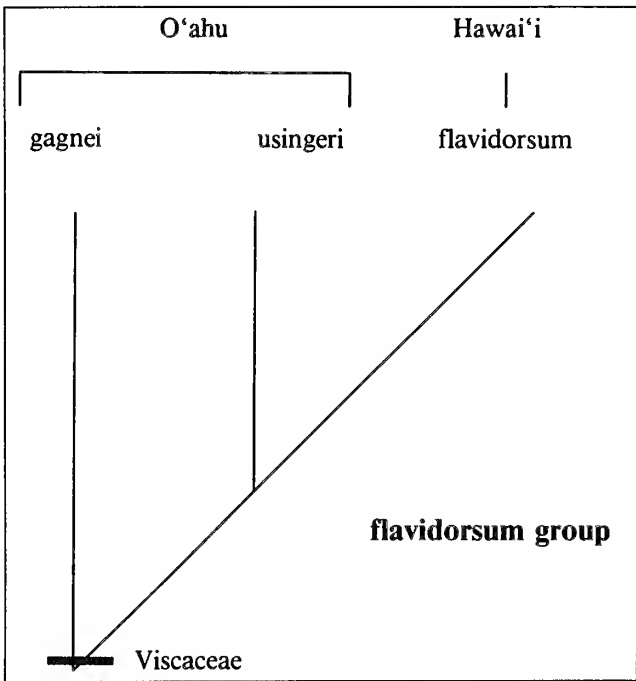


FIGURE 7.9. Relationships, distributions, and host plant associations in the *flavidorsum* species group.

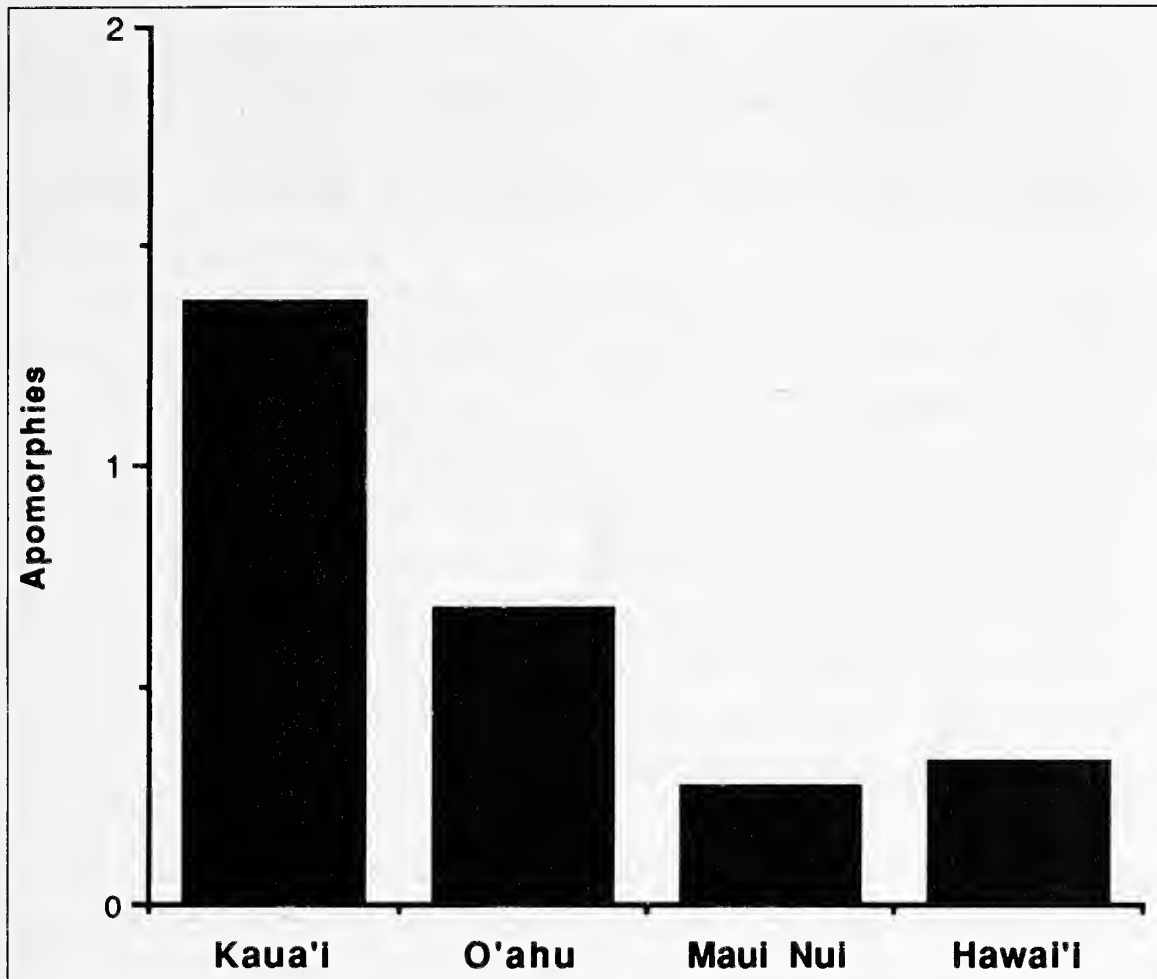


FIGURE 7.10. Average number of strong autapomorphies per species on different islands or island groups (Maui Nui complex).

This may explain the basal origin of *S. mokiha* and the tenuous monophyly of the *Kaua'i* group.

With the exception of *Sarona alani*, which certainly represents an independent colonization, the number of colonization events from *Kaua'i* to other islands is conjecture. All non-*Kaua'i* species or species groups originate from an unresolved basal polytomy. The absence of a *Kaua'i* sister group to any of the non-*Kaua'i* species groups and the group polytomy may suggest a single common origin for all non-*Kaua'i* species, but there is no synapomorphy that unites them.

Most O'ahu species are members of the monophyletic O'ahu group (node 6). Within this group, all species occur on O'ahu with the exception of *Sarona adonias*, the most derived species, which is found on the Maui Nui complex and Hawai'i (see Figure 7.8). The *flavidorsum* group also appears to have originated on O'ahu, with a subsequent colonization of Hawai'i (see Figure 7.9). These two species, *S. adonias* and *S. flavidorsum*, are the only confirmed examples of colonization from O'ahu to younger islands, and both are from O'ahu to Hawai'i, skipping the Maui Nui

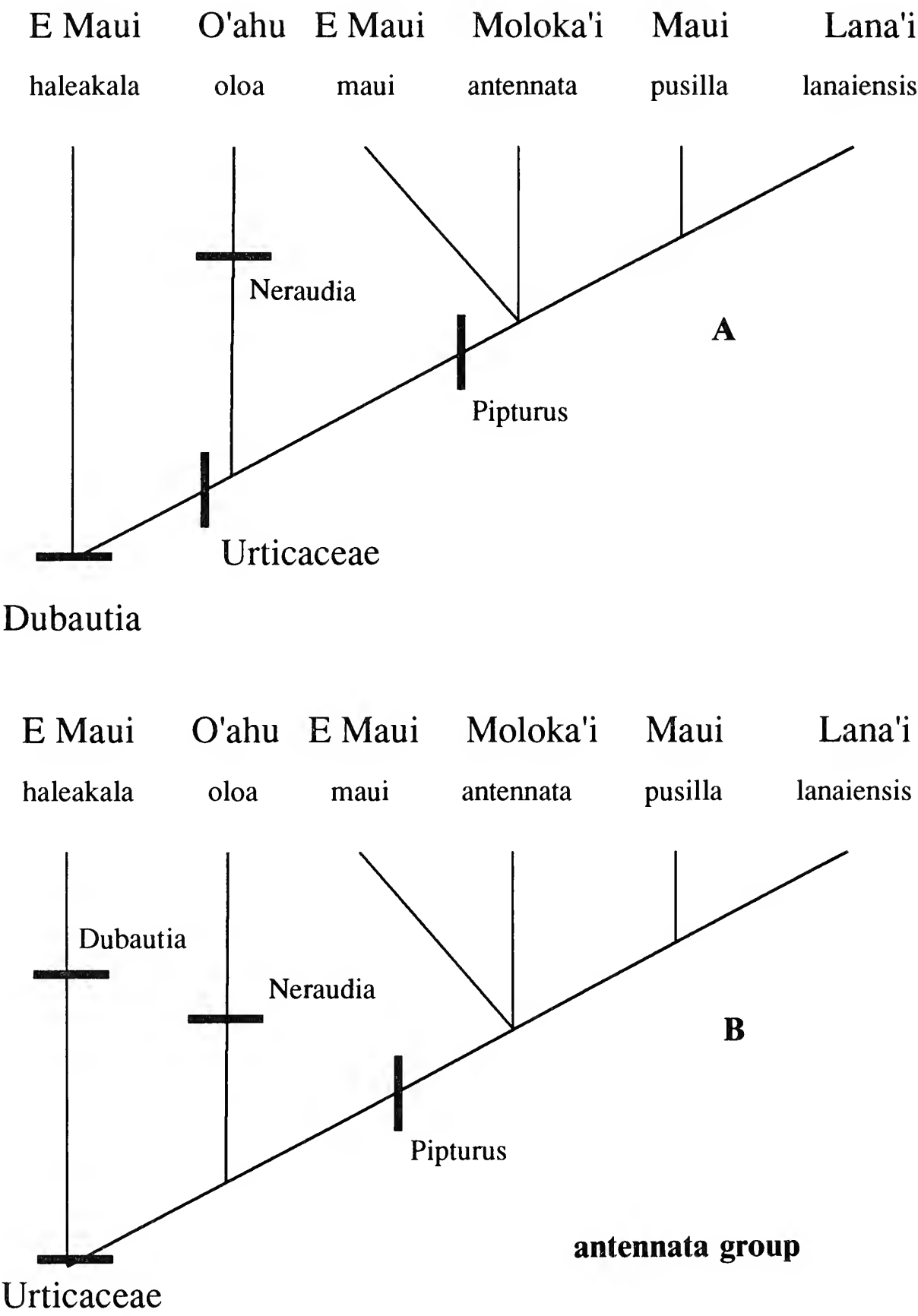


FIGURE 7.11. Relationships, distributions, and host plant associations in the *antennata* species group. (A) and (B) represent alternative hypotheses for the evolution of host plant preference in this group.

complex (see below for *S. adonias*). O‘ahu also appears to have been colonized at least once from the younger islands. *Sarona oloa* belongs to the *antennata* group, which either originated on the Maui Nui complex or colonized that area twice from O‘ahu, which is a less-parsimonious hypothesis (Figure 7.11).

Representatives of at least five distinct clades are found on the Maui Nui complex. For only one species, *Sarona adonias*, is the island of origin clear. Although *S. kuaana*, the sister species of *S. adonias*, is found on O‘ahu, the Maui Nui populations of *S. adonias* appear to be derived from the Hawai‘i populations. This is based on the fact that the Hawai‘i populations have the apex of the spicula expanded and serrate, as in *S. kuaana* and their sister species *S. xanthostelma*, whereas populations of *S. adonias* on the Maui Nui complex have the derived condition of a reduced and almost entire apex of the spicula (Asquith, 1994b), suggesting that *S. adonias* on the Maui Nui complex originated from Hawai‘i, not O‘ahu.

Of the other species groups found on Maui Nui, the *dakine* group (node 17), the *azophila* group (node 22), and the *kanaka* group (node 21) may have originated from a single colonization. The interpretation of the synapomorphy that unites these groups is equivocal, however (see discussion in Phylogenetic Analysis), which means Maui Nui could have received up to five independent colonizations. The *antennata* group is clearly monophyletic and unrelated to other groups. Although this clade displays high resolution of relationships among its component species (Figure 7.11), there are still several equally parsimonious hypotheses of its biogeographic history within the Maui Nui complex. The hypothesis requiring the least number of colonizations would place an ancestral taxon on Maui, followed by single colonizations to Moloka‘i and Lana‘i.

The island of Hawai‘i received four independent colonizations of *Sarona*. As previously mentioned, *S. alani* probably had a Kaua‘i or possibly O‘ahu origin, and *S. adonias* and *S. flavidorsum* are both derived from O‘ahu ancestors. The *myoporicola* group is the only example in *Sarona* of a probable origin of an Hawai‘i Island group on the Maui Nui complex.

Most species of *Sarona* are widespread within an island, and there is little evidence for the high provinciality displayed by other groups of insects such as the *Rhynchogonus* weevils (Swezey, 1934). There are a

few patterns of endemism within islands, however, usually involving individual volcanoes or mountain ranges.

On Kaua'i, the Makaleha Mountains are an area of endemism for the plant bug genus *Nesiomiris* (Gagné, in press) and the Ha'upu Ridge harbors endemic crickets (R. Rice, unpubl.). In *Sarona*, however, all species are restricted to the plateau area between Mount Wai'ale'ale and the Napali coast, with the exception of *S. akoko*, which also occurs in the Ha'upu range (Asquith, 1994b).

The Wai'anae and Ko'olau mountain ranges on O'ahu each harbor endemic species in many groups of insects (Hardy, 1965; Zimmerman, 1978; Otte, 1989). Half the O'ahu species of *Sarona* are known from both ranges. Three species are restricted to the Wai'anae Mountains, and two are found only in the Ko'olau Mountains. I know of no examples of intra-island allopatry among insects on Moloka'i and Lana'i, and all species of *Sarona* are restricted to eastern Moloka'i and central Lana'i.

East and West Maui are biogeographically distinct and are usually considered separate islands in this regard (Howarth, 1990). Only three species of *Sarona* are known from both East and West Maui. Surprisingly, the other four species are restricted to East Maui, and there are no known West Maui species.

At least four of the five volcanoes on the island of Hawai'i harbor endemic insects, Mauna Kea, Mauna Loa, the Kohala Mountains, and Hualalai (Howarth, 1990). Six of nine *Sarona* species are widespread on Hawai'i or occur on more than one volcano. *Sarona alani* is restricted to the windward slopes of Mauna Loa, *S. flavidorsum* is found only in the leeward Kohala Mountains, and *S. iki* known only from the windward Kohala Mountains.

An important cautionary note when interpreting the above-mentioned patterns of within-island distributions is the lack of adequate sampling for many areas and species. *Sarona* has not been collected from the Makaleha Mountains on Kaua'i, for example, yet they are higher than 1,000 m in elevation and are a known area of endemism for *Nesiomiris* (Gagné, in press). Also, many of the species of *Sarona* on O'ahu and Maui are known only from one or two collections. Therefore, I suspect that with more collecting, additional restricted endemics may be discovered, and the ranges of most species will be documented as broader than presently known (i.e., species distributed on all volcanoes of O'ahu and Maui).

HOST PLANT—HABITAT EVOLUTION

Species of *Slaterocoris* and *Scalponotatus*, the sister group to *Sarona*, breed primarily on species of Asteraceae in open, mesic to dry habitats. Half the Kaua'i species of *Sarona*, plus *S. alani* (an enigmatic primitive species on Hawai'i) and *S. hie* (a primitive member of the O'ahu group), are associated with the Rutaceae genus *Melicope* (formerly *Pelea*) (Stone et al., 1990) (see Table 7.1). A striking feature of all the *Melicope*-associated species, except *S. kukona* and possibly *S. alani*, is that they inhabit wet, high-elevation forest. Although derived when compared with its extra-Hawaiian sister group, I hypothesize that this wet forest *Melicope* association is plesiomorphic for *Sarona*, at least for the taxa on the present high islands. On Kaua'i, there has been only one major host plant shift. *Sarona annae*, the primitive member of the Kaua'i group, breeds on *Zanthoxylum*, another genus of the Rutaceae (see Figure 7.7), whereas the derived sister species in this clade, *S. akoko* and *S. laka*, breed on *Chamaesyce* and *Claoxylon*, respectively, both in the Euphorbiaceae. With this host plant switch has been a concomitant change in habitat from wet/mesic forest to mesic/dry habitat. *Sarona kukona* has also shifted from the initial wet forest habitat and is now associated with *Melicope barbigera* in the drier portions of diverse mesic forest on Kaua'i.

Host plant and habitat relationships within the *adonias* group on O'ahu are poorly understood. If the unconfirmed host of *Sarona hie* is indeed *Melicope*, then a *Melicope* association is probably plesiomorphic for the *adonias* group. The only confirmed host plant shifts in the *adonias* group from a presumably primitive *Melicope* association is *Sarona kaala*, which breeds on *Broussaisia arguta* in wet forest, and *S. adonias*, associated with *Metrosideros polymorpha* in wet to mesic forest (see Figure 7.8). However, until the host plant association of the *S. adonias* sister taxon, *S. kuaana*, is determined, we cannot know if the switch to *Metrosideros* occurred before or after the inter-island colonization by *S. adonias* or its ancestor. In the *flavidorsum* group, at least *S. flavidorsum* and *S. gagnei* are associated with the hemiparasitic genus *Korthalsella* (Viscaceae) (see Figure 7.9). Although *Korthalsella* can be found associated with a number of different woody plants (Wagner et al., 1990), the *Korthalsella* plants from which *S. flavidorsum* and *S. gagnei* have been collected were attached to *Acacia koa* A. Gray (Fabaceae) in mesic to dry forest.

The host associations of the *dakine* and *kanaka* groups on the Maui Nui complex are unknown, but both groups appear to have

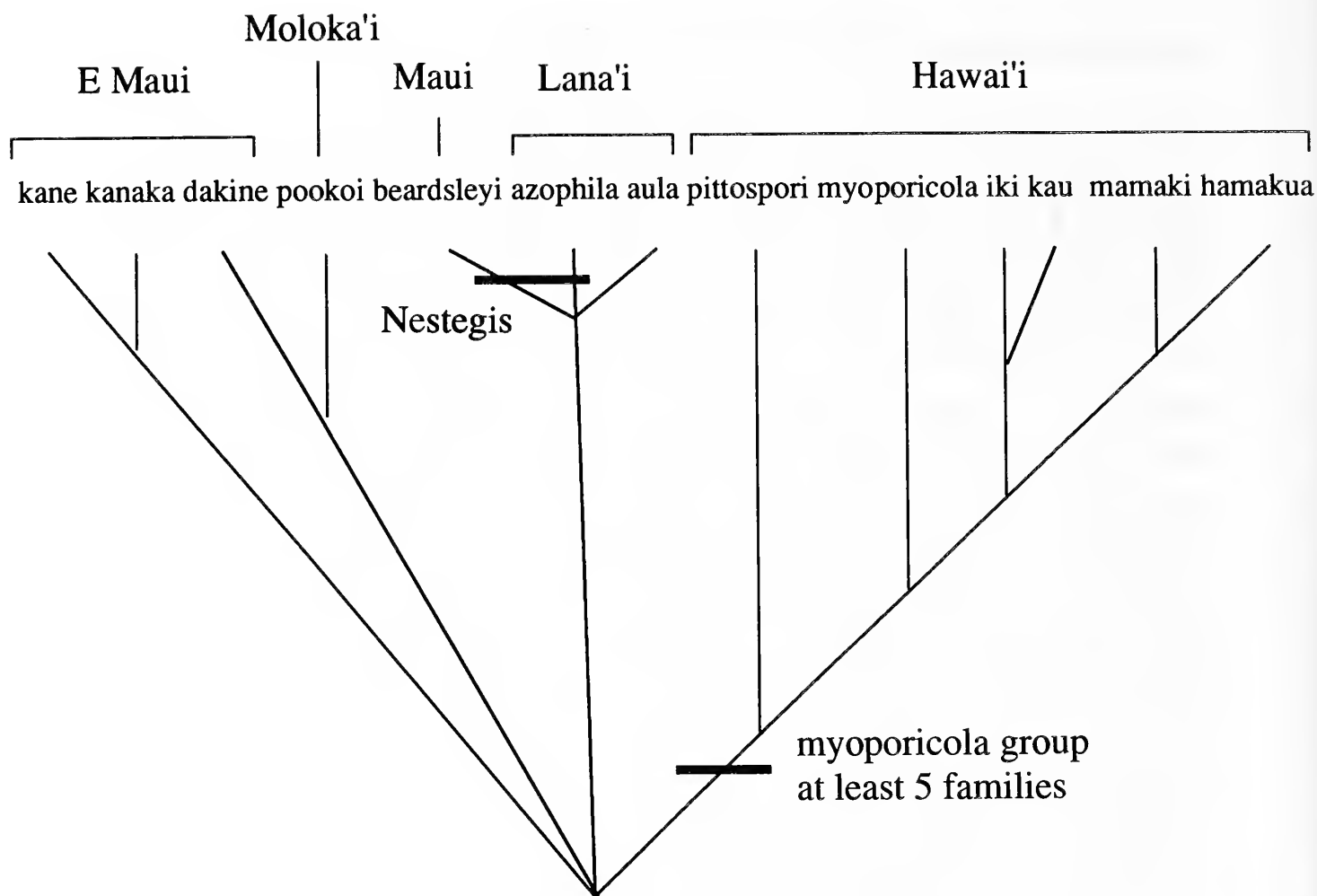


FIGURE 7.12. Relationships, distributions, and host plant associations in the *myoporicola* species group and smaller clades. This group is the best example of host-mediated speciation, with species of the *myoporicola* group on at least five different families of plants.

retained wet forest habitat preferences. The evolution of the *azophila* group has involved major switches in both host plant and habitat preferences. All three species occur in drier mesic or dry forests on *Nestegis sandwicensis* (Oleaceae) and *Ilex anomala* (Aquifoliaceae) (Figure 7.12).

With the exception of *Sarona haleakala*, which breeds on *Dubautia menziesii* (Asteraceae) in alpine dry shrubland on East Maui, all species in the *antennata* group are associated with Urticaceae in wet to mesic forest or gulches (see Figure 7.11). If the association of *S. haleakala* with *Dubautia* is plesiomorphic, the origin of the lineage was not tied to an Urticaceae host (see Figure 7.11A). Alternatively, although *S. haleakala* is the most primitive member of the group, its habitat is certainly highly autapomorphic, as may be its association with *Dubautia* (see Figure 7.11B).

In contrast to all other species groups, which have made relatively few major host plant switches (sister species typically breed on hosts in the same genus or family), members of the *myoporicola* group are associated with at least five different plant families (Figure 7.12). This clade has also made colonizations of the Urticaceae and Asteraceae independent of that by the *antennata* group. The *myoporicola* group also occupies a diverse array of habitats, from wet and mesic forest (*Sarona mamaki* and *S. hamakua*) to subalpine dry forest (*S. myoporicola*) and dry shrubland (*S. kau*).

SPECIATION

The data available to most systematists, phylogenetic relationships and distributions, are sufficient to test predictions of different geographic models of speciation (Lynch, 1989; Asquith, 1993). Following Lynch (1989), I argue that if we examine only sister taxa and there are no available data to the contrary, then contemporary distributions reflect the geographic origins of the species involved; thus, sympatric taxa arose in sympatry and allopatric taxa arose in allopatry. I do not suggest that the distributions of taxa never change or that extinction does not occur. Climatic change clearly resulted in elevational movement of plant communities in Hawai'i (Gavenda, 1992), and undoubtedly, their insect faunas experienced similar changes. Likewise, if *Sarona* originated on a pre-Kaua'i island as I have argued, then the taxa endemic to those older islands are now extinct. If data on past distributions or extinct taxa become available, they should certainly be used; however, these arguments need not be invoked as ad hoc explanations in the absence of any evidence.

There appear to be at least three distinct geographic modes by which species of *Sarona* have originated in Hawai'i: allopatrically by colonization of new islands, allopatrically by isolation on volcanoes or mountain ranges, and sympatrically by colonization of new host plants. These modes are not mutually exclusive, and new host associations may have coincided with a colonization of a new island. For example, *Sarona oloa* colonized O'ahu from an ancestor on the Maui Nui complex and switched from a *Dubautia* or *Pipturus* host to *Neraudia* (see Figure 7.11). Most inter-island colonists, however, seem to have retained the ancestral host association.

Inter-island allopatric speciation can clearly be seen in sister taxa such as *Sarona kuaana* on O'ahu and *S. adonias* on the Maui Nui

complex and Hawai'i. Interestingly, half the allopatric speciation events have not occurred between adjacent islands but between Kaua'i or O'ahu and Hawai'i. This may be because the frequency of allopatric speciation within the Maui Nui complex is underestimated, due to uncollected species on some islands. It is likely, for example, that a *Nestegis*-associated species in the *azophila* group occurs on Moloka'i (Figure 7.12). Although these discoveries would increase the total number of allopatric events between adjacent islands, there would still be few examples of O'ahu–Maui Nui speciation events.

Allopatric speciation within Maui Nui has probably been more complicated than the older-to-younger pattern among other islands. Basal species in Maui Nui clades do not usually occur on the oldest island of the complex (Moloka'i). Also, even more so than other island colonizations, intra-island speciation within Maui Nui has not usually involved concomitant host plant switches, exemplified by the *antennata* group (see Figure 7.11). This pattern may reflect very different isolation histories within Maui Nui compared with isolation between other islands. Changes in sea level during periods of glaciation repeatedly united and separated the islands composing Maui Nui (Zimmerman, 1948; see also Carson and Clague, this volume, Chapter 2). Thus, true vicariance, in the form of fragmentation of the ancestral distribution, may explain the unique pattern observed in the Maui Nui complex.

Although a few species of *Sarona* are restricted to volcanoes or mountain ranges within an island (see Biogeography section), in most cases their sister taxa either occur on other islands (*S. kuaana* and *S. adonias*; *S. flavidorsum* and *S. usingeri*) or encompass the isolate on the same island (*S. antennata* and *S. pusilla* plus *S. lanaiensis*). The only presumed case of allopatric speciation within an island is *S. oahuensis* in the Wai'anae Mountains and its sister species *S. kohana* in the Ko'olau range (see Figure 7.8). Another possible case is *S. iki* in the Kohala Mountains of Hawai'i and its sister species *S. kau*, restricted to leeward Mauna Kea and Mauna Loa (Figure 7.12). Both these cases should be considered tentative, however, as both *S. oahuensis* and *S. iki* are known only from single collections.

With the possible exception of *Sarona kau* and *S. iki* mentioned above, all sister taxa in the *myoporicola* group are largely sympatric on Hawai'i and breed on different host plants, providing the strongest case for sympatric host plant speciation. Host plant switches appear to have been common in *Sarona*, however, and possible cases of sympatric speciation are known from all islands except Moloka'i.

Sympatric speciation by host plant has generally occurred by colonizing a new but taxonomically related host. In the *Kaua'i* group, for example, four species of *Sarona* are each specific to species of *Melicope* (see Table 7.1) and can be found syntopically. The sister species *S. saltator* and *S. hiiaka* are both restricted to *Melicope clusiifolia*, with no apparent partitioning by season or plant part used. This is the only case of sympatric species found on the same species of host plant. Similar examples of colonization between taxonomically proximate hosts are seen in *S. akoko* and *S. laka*, which both feed on different genera of Euphorbiaceae, and *S. oloa*, which breeds on *Neraudia* and its sister taxa on *Pipturus*, both in the Urticaceae. Other sympatric host-mediated speciation events have occurred between taxonomically unrelated hosts. The *myoporicola* group is the best example of this pattern, with its constituent species occurring on plants in five different families (Figure 7.12).

If we assume *Sarona* to have originated on an older, pre-Kaua'i island and that the ancestor of all Kaua'i species originated from a single allopatric speciation event, then 40% of speciation events known to have occurred subsequently can be attributed to inter-island allopatric speciation events (Table 7.2). Nineteen events (54% of speciation in *Sarona*) have been sympatric, likely precipitated by host plant switches, whereas only two or three examples of intra-island allopatry are recognized. This is probably a conservative estimate of the frequency of sympatric speciation, because the origins of all basally originating clades were attributed to inter-island colonizations. Some of these lineages, however, such as the *Kaua'i* group, could have sister taxa on the same islands, which means sympatric speciation could account for as much as 60 to 70% of speciation in *Sarona*.

DISCUSSION

The conclusion seems inevitable that geographic isolation or host isolation or both may be sufficient to set in operation the processes of species formation.

—USINGER, 1942

The general pattern of evolution that has given rise to most extant species of *Sarona* appears to be one of colonization from older to younger islands, with subsequent sympatric, host-mediated speciation on the newly colonized island (Figure 7.13). The colonization of new islands and

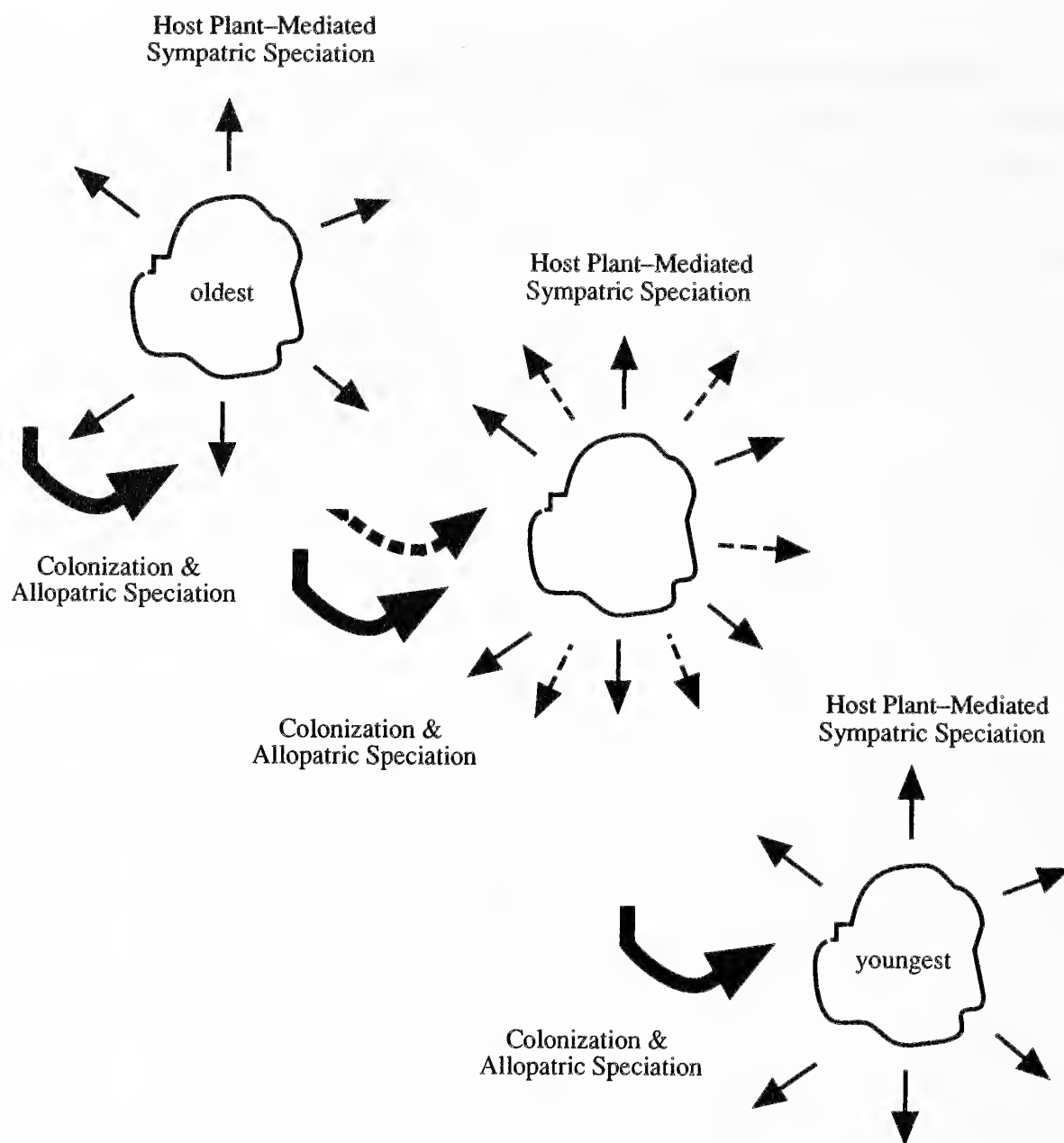


FIGURE 7.13. Evolution of *Sarona*, showing an age sequence of three islands. *Large solid arrows* indicate primary inter-island colonization and speciation events. *Large broken arrow* indicates secondary inter-island colonization and speciation event. *Small solid arrows* indicate sympatric speciation by colonization of new host plants. *Small broken arrows* indicate sympatric speciation on new host plants by lineage resulting from secondary inter-island colonization.

coincident speciation are not surprising, as it is the most commonly held view of evolution in Hawaiian organisms (Carson, 1987b).

The proposed prevalence of sympatric speciation in this group of insects may be surprising to some biologists. Despite the vociferous arguments against the possibility and frequency of sympatric speciation (Mayr, 1963, 1976, pp. 144–175; Futuyma and Mayer, 1980), there exists ample evidence for this mode among insects (for a review, see Tauber and Tauber, 1989). Both theoretical and empirical arguments are particularly strong for

TABLE 7.2. Categorized Speciation Events in Five Genera of Phytophagous Hawaiian Insects

| Type of speciation event ^a | <i>Sarona</i> (40 spp.) | <i>Oceanides</i> (25 spp.) | <i>Neseis</i> (33 spp.) | <i>Plagithmysus</i> (136 spp.) | <i>Nesiomiris</i> (50 spp.) |
|---------------------------------------|----------------------------|-------------------------------|----------------------------|-----------------------------------|--------------------------------|
| Sympatric, total | 19 | 2 | 3 | 22 | 8 |
| Same host | 1 | 0 | 3 | 10 | 1 |
| Different host | 10 | 2 | 0 | 12 | 7 |
| Inter-island, total | 14 | 8 | 15 | 34 | 14 |
| Same host | 5 | 8 | 13 | 30 | 14 |
| Different host | 2 | 0 | 2 | 4 | 0 |
| Intra-island, total | 2 | 0 | 2 | 2 | 9 |
| Same host | 1 | 0 | 2 | 2 | 9 |
| Different host | 1 | 0 | 0 | 0 | 0 |

Note: Because hosts are not known for all species, the total number of speciation events in any geographic category is not the sum of the host categories.

^a“Host” categories refer to whether sister taxa feed on the same or a different host plant.

phytophagous insects (Bush, 1969, 1974; Bush and Diehl, 1982; Diehl and Bush, 1989). Thus, although it may seem somewhat heretical to propose extensive sympatric speciation for a group in the Hawaiian Islands renowned for its examples of allopatric speciation, it will probably come as no surprise to other students of species-rich phytophagous groups.

In the spirit of this book, a more important question is whether the pattern seen in *Sarona* is also common to other phytophagous insects in Hawai‘i. Unfortunately, even the alpha taxonomy of most Hawaiian groups is grossly inadequate to fully explore this question. I found only four genera, in addition to *Sarona*, whose classifications have been revised and for which at least phenetic hypotheses of relationships are available (Table 7.2). *Nesiomiris* is another endemic group of orthotyline plant bugs that, like *Sarona*, feed on leaves and reproductive tissues of their host plants and the only other group with a cladistically derived phylogeny (Gagné, in press). *Plagithmysus* is an endemic group of long-horned beetles (Cerambycidae) whose larvae bore in the stems and branches of their host plants (Gressitt, 1978). *Neseis* and *Oceanides* are endemic genera of seed bugs (Lygaeidae), which feed on the seed heads of

their host plants (Usinger, 1942). For the last three taxa, only phenetically constructed phylogenies are available; therefore, I have restricted my examples to what the authors indicated are sister species, with the belief that at this level, classical taxonomy is probably not much different from cladistics (Boucot, 1979).

Compared with these other groups, *Sarona* is unusual in the preponderance of sympatric speciation. Although there are examples of sympatric speciation in all the groups, it is the dominant mode only in *Sarona* (Table 7.2). The pattern for most sympatric events is that the two daughter species are restricted to different host plants, again suggesting host-mediated speciation. Only in *Nesiomiris* and *Neseis* are there multiple examples of sympatric speciation on the same species of host.

Most speciation in all groups except *Sarona* has been allopatric between islands. Also, most sister taxa occur on the same host. In *Oceanides*, for example, there are several groups for which the component species all breed on the same host plant, but each species is endemic to a different island (Usinger, 1942). In contrast to the pattern proposed for *Sarona* then (Figure 7.13), these other taxa appear to first colonize a new host plant and then subsequently colonize new islands and speciate allopatrically, retaining the ancestral host association. This process even appears to have been repeated within a genus by different clades using the same host. *Neseis hiloensis* and *N. nitidus*, for example, are both restricted to *Pipturus*, and both have radiated allopatrically, with taxonomically distinct forms on all islands (Usinger, 1942). Intra-island allopatry has been infrequent in all groups, with the possible exception of *Nesiomiris*, which has complex patterns of distribution, particularly on O'ahu (Gagné, in press). Variation in the frequency of intra-island allopatry cannot be attributed entirely to variation in dispersal capabilities, because *Sarona* and *Plagithmysus* are as easily dispersed or less so than *Nesiomiris* but have fewer geographically restricted species.

Just as the linear pattern of island formation provides a basis from which to hypothesize common patterns of allopatric speciation, the colonization and speciation sequence of host plants may result in congruent patterns of speciation among their insect commensals. For example, the radiation of *Sarona* on different species of *Melicope* is paralleled by the leaf-mining Opostegidae (Lepidoptera) (Zimmerman, 1978), and both *Nesiomiris* (Gagné, 1983) and the weevil genus *Nesotocus* (Coleoptera: Curculionidae) (Swezey, 1954) are largely or exclusively restricted to Araliaceae hosts; unfortunately, the relevant phylogenies are not available to allow a search for congruent speciation patterns.

The plants in the Hawaiian Islands with the greatest number of associated phytophagous insects are *Metrosideros polymorpha*, *Acacia koa*, and *Pipturus* spp. (Swezey, 1954), largely due to their abundance and ubiquity (Southwood, 1960). In addition to harboring large numbers of individual species, there have clearly been radiations on each of these host plants, with *Pipturus*, for example, harboring several allopatric sister species of *Sarona*, *Plagithmysus*, and *Neseis*, as well as the genera *Nesodyne* (Homoptera: Delphacidae) and *Philodria* (Lepidoptera: Gracillariidae) (Zimmerman, 1978). The host plant groups have not radiated extensively themselves, however, and I am unaware of any insects restricted to the few segregate species of *Pipturus* or *Metrosideros*. Similarly, with the exception of *Sarona oloa* on *Neraudia*, other genera of Urticaceae do not harbor taxa related to the *Pipturus*-associated species in these genera. Thus, the likelihood of colonization of a common host such as *Pipturus* is not determined solely by its taxonomic affinities. This is further supported by the fact that there have been multiple, independent colonizations of *Pipturus* by at least *Sarona*, *Plagithmysus*, and *Neseis*, each time from unrelated ancestral hosts. Thus, the incongruence of island colonization and speciation among these insect groups is paralleled by their disparate patterns of host plant colonizations and speciation.

In summary, the only evolutionary pattern in *Sarona* that is typical of what is known of other Hawaiian organisms is the older-to-younger island direction of colonization, and even this pattern is dependent largely on my argument of expected distribution of autapomorphies. Also, the evolution of *Sarona* may not even be typical of other phytophagous insect groups. But just as I am not surprised to find that *Sarona* speciates sympatrically, we should also not be surprised at the disparity of evolutionary patterns among various phytophagous groups. A multitude of species have evolved in the Hawaiian Islands (Howarth, 1990). They have evolved through a plurality of speciation modes, resulting in a diversity of evolutionary patterns.

ACKNOWLEDGMENTS

I greatly benefited from discussions with Frank Howarth and Dan Polhemus about the Hawaiian insect fauna. I am particularly indebted to all those people who collected specimens of *Sarona* through the years. Gary Stonedahl, Dan Polhemus, Frank Howarth, Rosemary Gillespie, Mike Kido, Ken Kaneshiro, and Kerry Shaw kindly provided reviews of

the manuscript. My wife, Anna, produced the fine habitus illustrations, and her unflagging support of this and other projects is acknowledged. This work was carried out while I was a research associate in the Department of Entomology, University of Hawaii.

APPENDIX 7.1. Character List for *Sarona*

Characters 4 and 20 are unordered.

Right Paramere

0. 0 = variously modified but never as follows; 1 = large, weakly laterally flattened, with basal arm absent.
1. 0 = variously modified but never as follows; 1 = ventral arm of paramere reduced and dorsal arm developed so that paramere is C- or L-shaped as in *Sarona annae*.
2. 0 = variously modified but never as follows; 1 = acuminate with basal arm arising medially and thickened; 2 = acuminate, basal arm arising medially and thickened, apex of main arm abbreviated.
3. 0 = variously modified but never as follows; 1 = cylindrical, acuminate, without basal arm; 2 = very short, apex strongly tapered.
4. 0 = variously modified but never as follows; 1 = ventral arm of paramere reduced and basal arm erect and straight so that paramere is somewhat L-shaped; 2 = with basal arm erect and curved distally so that paramere is C-shaped; 3 = with basal arm erect, short, main arm reduced to equal to or less than length of basal arm, as in *S. dakine*.
5. 0 = variously modified but never as follows; 1 = if paramere C-shaped, both arms of equal size.
6. 0 = medial arm entire; 1 = medial arm dentate.
7. 0 = without protuberance or teeth on ventral margin; 1 = with protuberance, teeth, or short arm on ventral margin.

Left Paramere

8. 0 = with medial flange apically; 1 = flange absent.
9. 0 = basal angle not or poorly developed; 1 = basal angle greatly developed, height greater than width.
10. 0 = arm with apex modified but never as follows; 1 = arm with distinct but small swelling preapically.

Genital Capsule

11. 0 = a single tergal process present on the right dorsal margin; 1 = a small secondary tergal process present on the left dorsolateral margin; sometimes present only as a sharp angle.

12. 0 = secondary tergal process absent, primary process near lateral margin of capsule; 1 = primary tergal process near midline; 2 = a small secondary tergal process present on the dorsal margin, just left of the midline, primary tergal process large; 3 = both tergal processes of equal size.
13. 0 = primary tergal process present; 1 = tergal process lost.
14. 0 = right tergal process variably modified but never as follows; 1 = right tergal process reduced to 2 short teeth at far right dorsolateral margin.
15. 0 = right tergal process variably modified but never as follows; 1 = right tergal process straight, slightly elongate, almost at right angle to margin.
16. 0 = posteroventral margin weakly convex; 1 = posteroventral margin strongly convex.
17. 0 = posteroventral margin weakly convex; 1 = posteroventral margin narrowed and acuminate.

Vesica

18. 0 = spicula variously modified but never as follows; 1 = spicula elongate distally and weakly sinuate, apex of flange reduced or absent.
19. 0 = spicula variously modified but never as follows; 1 = spicula elongate distally and weakly sinuate, apex of flange digitiform.
20. 0 = spicula variously modified but never as follows; 1 = spicula slightly reduced distally, not sinuate, apex of flange not modified; 2 = spicula strongly reduced distally, not sinuate, apex of flange reduced; 3 = spicula strongly reduced distally, not sinuate, apex of flange slightly acuminate.
21. 0 = spicula variously modified but never as follows; 1 = spicula reduced distally, straight, apex of flange not modified; 2 = spicula more strongly reduced distally.
22. 0 = apex of spicula serrate; 1 = apex of spicula entire.

Vestiture and Body

23. 0 = all setae simple; 1 = simple setae mixed with sericeous setae.
24. 0 = female with simple setae around base of ovipositor; 1 = female with modified setae around base of ovipositor.
25. 0 = dorsal coloration solid dark; 1 = dorsal coloration pale yellow.
26. 0 = pro- and mesofemora with solid coloration; 1 = all femora banded.
27. 0 = antennae narrow, cylindrical; 1 = second antennal segment strongly swollen.
28. 0 = antennal segment II solid colored or basal half differently colored than distal half; 1 = segment II colored at base and apex only.
29. 0 = antennal segment IV solid colored in male; 1 = segment IV pale basally.
30. 0 = margins of hemelytra weakly arcuate; 1 = margins of hemelytra strongly arcuate.

8

Comparison of Speciation Mechanisms in Web-Building and Non-Web-Building Groups within a Lineage of Spiders

ROSEMARY G. GILLESPIE AND
HENRIETTA B. CROOM

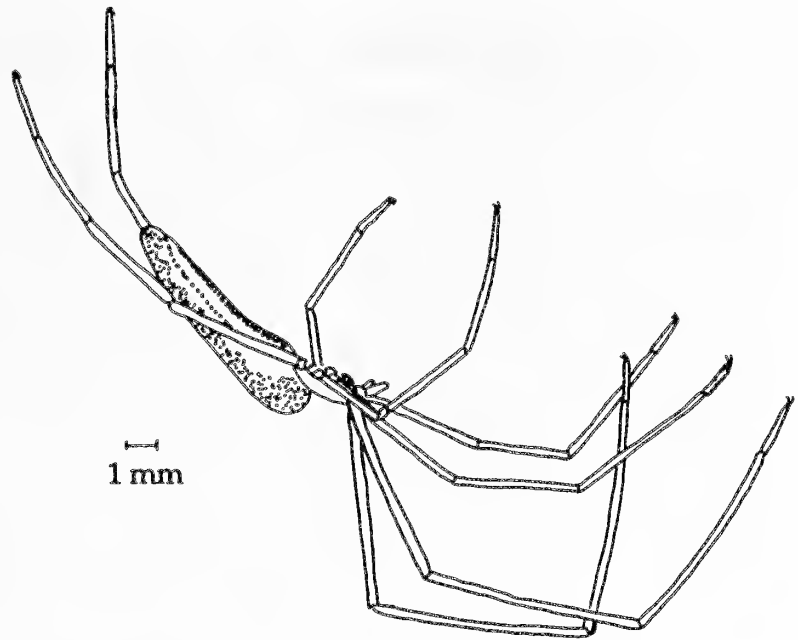
The formation of new species is a key element to evolutionary advancement and diversification (Mayr, 1963). The traditional mechanisms proposed for speciation generally include allopatry as an important element in the initial divergence of incipient species (Mayr, 1963; Futuyma and Mayer, 1980; Paterson, 1981, 1982; Carson, 1986). However, several studies have argued that strict geographic isolation is not necessary under conditions in which disruptive selection might operate to allow divergence between broadly contiguous habitats (Wood, 1980; Bush and Howard, 1986; Wood and Keese, 1990). Disruptive selection may be strong enough to lead to speciation only when environmental heterogeneity is strong, range of available food resources is broad, difference between habitat extremes is large and persistent, and populations demonstrate considerable genetic variability (Grant and Grant, 1989). The operation of disruptive selection may be enhanced if the taxa under question are habitat specialists, and species may form more rapidly under such conditions than they do in allopatry (Thoday, 1972; Rosenzweig, 1978; Wood and Guttman, 1982; Bush and Howard, 1986). When adaptive radiation is prevalent, such as frequently occurs in isolated archipelagoes, parapatric speciation by disruptive selection may be the most reasonable means by which speciation might occur (Rosenzweig, 1978). Disruptive selection does indeed appear to underlie speciation in certain Galápagos finches (Grant and Grant, 1989) as well as among the Hawaiian carabid beetles (J. K. Liebherr, unpubl.) and Hawaiian crickets (Otte, 1989).

Another source of contention regarding the speciation process involves the mode of reproductive isolation once incipient species have diverged. In particular, what is the relative importance of ecological and associated behavioral shifts versus sexual selection in enforcing reproductive isolation? For example, when species are released from interaction with related species, by whatever means, they often broaden their habitat use and exhibit much more individual variation within species (Grant, 1966; Lack, 1971; McCune, 1990). Reproductive isolation may then occur as a consequence of ecological changes in allopatry (Soans et al., 1974; Hurd and Eisenberg, 1975; Kiliyas et al., 1980; Markow, 1981; Dodd, 1989; Rice and Salt, 1990). If such reproductively isolated incipient species were reunited with their parents, selection could act on this variability to minimize the resources jointly used by both species and would lead to further ecological divergence (Mayr, 1963; Grant, 1986). Alternatively, when species are released from interaction with related species, their sexual behavior can become simpler, with more intraspecific variability (Kaneshiro, 1983; Otte, 1989). Sexual selection may then operate to cause reproductive divergence of the incipient species during isolation (Carson and Kaneshiro, 1976; Carson, 1986). Differences in sexual behavior may be accentuated when such isolated incipient species are reunited with their parents.

The Hawaiian Islands offer a unique opportunity for examining microevolutionary events culminating in the formation of species, largely because their extreme isolation has allowed repeated explosive diversification of species from single ancestors (Simon, 1987). Such rampant speciation is well illustrated in Hawaiian birds (Berger, 1981; Freed et al., 1987), land snails (Cooke et al., 1960), crickets (Otte, 1989), and flies (Carson and Kaneshiro, 1976; Kaneshiro and Boake, 1987). These radiations are associated with high frequencies of endemism: greater than 81% in birds (Pratt et al., 1987) and an extraordinary 99% in terrestrial mollusks (Gagné, 1988) and arthropods (Gagné and Christensen, 1985). Moreover, the islands themselves are a series of volcanoes arranged within an identifiable chronological time frame, ranging from Kaua'i, the oldest and most eroded of the current high islands, to Hawai'i, the youngest, largest (with five volcanoes), and highest island (Heliker, 1989). It is therefore reasonable to consider the archipelago as a series of historical snapshots, with speciation being currently instigated on the youngest island and progressively developing through the older islands to the north.

FIGURE 8.1.

Tetragnatha elongata, a typical representative of the genus *Tetragnatha* from the continental United States, occurring in riparian habitat.



Our research has focused on spiders in the long-jawed orb-weaving genus *Tetragnatha* (Figure 8.1), one of the most widespread of all spider genera (Levi, 1981). Representatives of the genus are remarkably homogeneous in both morphology, with elongate bodies and legs (Kaston, 1948), and ecology (Dabrowska Prot and Luczak, 1968a,b; Dabrowska Prot et al., 1968). *Tetragnatha* build orb webs with open hubs (Wiehle, 1963), the structures being extremely light and fragile with low adhesiveness (Yoshida, 1987). They are generally built over water or in other wet places (Levi, 1981; Gillespie, 1987a). During periods of inactivity, the spiders adopt a cryptic posture, with body and legs outstretched, on twigs and grasses. During activity, the spiders—being web-builders—generally behave as ambush predators. However, there is considerable variability in the amount of movement involved in foraging activity (Caraco and Gillespie, 1986; Gillespie, 1986; Gillespie and Caraco, 1987) and the extent to which a web is used to capture prey (Luczak and Dabrowska Prot, 1966; Levi, 1981; Shinkai, 1984; Gillespie, 1987b). Prey are captured by simply securing them in the chelicerae, and silk does not appear to be used for immobilization (Yoshida, 1987). There is no evidence of elaborate courtship before mating (Levi, 1981). On encountering each other, male and female *Tetragnatha* appear to be involved in a combative interaction, both with their chelicerae and fangs outstretched. If the sexual encounter is successful, the male locks the fangs of the female against the spur (apophysis) on the dorsal surface of his chelicerae. He then closes his fangs over those of the female, to lock the female securely in position. The chelical teeth themselves are not involved in this locking mechanism.

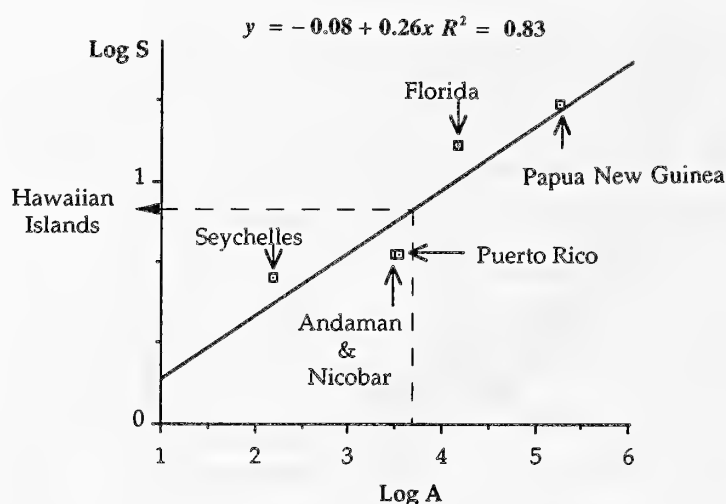


FIGURE 8.2. Log-log species-area relationship for the genus *Tetragnatha*, using numbers of species from various selected sites around the world.

In contrast to their worldwide homogeneity, *Tetragnatha* species from the Hawaiian Islands are very diverse. Because the genus has representatives on almost every land mass worldwide, it is possible to predict the number of species of *Tetragnatha* that would be expected to occur on a land mass the size of the Hawaiian Islands in the absence of autochthonous evolution. We can then assess the extent to which speciation has occurred within the archipelago. We used the model developed by MacArthur and Wilson (1967) relating number of species (S) to area (A) to determine the number of species expected for a given land mass, with the slope of the regression line being z , a dimensionless parameter typically in the value range of 0.18 to 0.35. We assessed the distribution and ecology of the genus *Tetragnatha* on various island systems in the same 10 to 25° N latitude range worldwide (Roewer, 1942; Bonnet, 1959; Brignoli, 1983; Platnick, 1989): Florida (Levi, 1981), New Guinea (Chrysanthus, 1975; Okuma, 1987), Andaman and Nicobar (Tikader, 1977), Puerto Rico (Petrunkévitch, 1930; Chickering, 1957; R. G. Gillespie, unpubl.), and the Seychelles (Benoit, 1978). We omitted any representatives that appeared to be anthropogenic introductions (i.e., recently discovered, widespread taxa that occur in disturbed habitats). The results indicated a strongly significant relationship between species and area, with a z value of 0.26, which falls well within the range of typical values (Figure 8.2). In all these situations, the representative species retained the characteristics of the genus—elongate body, legs, and chelicerae; riparian habitat; flimsy orb web; and only very few species endemic to any particular location. Based on this analysis, we would predict that an island system the size of the Hawaiian chain would have approximately eight species. However, the Hawaiian archipelago may hold as many as 100 or more species (R. G. Gillespie, unpubl.), although only a few of the Hawaiian taxa have

been described (1 species by Karsch, 1880; 8 species by Simon, 1900; and 16 species by Gillespie, 1991, 1992a). This suggests that the genus has radiated in a spectacular manner in the archipelago. Not only are the Hawaiian *Tetragnatha* highly species-rich, they are also diverse in morphology, ecology, and behavior. Although certain behaviors remain unchanged (e.g., their mating and prey-biting behavior and their cryptic posture), the Hawaiian taxa span a broad spectrum of colors, shapes, sizes, ecological affinities, and behaviors. For example, most of the Hawaiian *Tetragnatha* species build the orb web characteristic of the genus, and many of these taxa have become extreme habitat specialists. An entire branch of the lineage (the *spiny leg* clade), however, has modified its behavior; representatives are cursorial predators that have abandoned web-building. These cursorial species tend to be more generalized in terms of habitat preference.

A primary goal of this study was to determine the extent to which a given pattern of diversification and associated biogeography is affected by habitat association. Our prediction was that habitat specialists may diverge within an island, through the action of disruptive selection. Habitat generalists should generally diverge between islands. A second major goal was to assess the role of ecological and associated behavioral changes in the initial separation of incipient taxa.

To address these questions, we used both morphological and molecular information. We used mitochondrial DNA sequences to determine overall relationships of Hawaiian *Tetragnatha* species to each other and to congeners outside the islands. We then used morphological variation to examine relationships among taxa from two clades within the Hawaiian *Tetragnatha* lineage that differ in their level of habitat association: the *spiny leg* clade that never builds webs (Figure 8.3A) and another clade (which we will refer to here as the *elongate* clade) that builds orb webs characteristic of the genus (Figure 8.3B). We will assume that, because of their web-building behavior, representatives of the *elongate* clade tend to be more sedentary and have a greater propensity toward habitat specialization than representatives of the *spiny leg* clade. We tested the hypothesis that the differences in habitat utilization between the two clades allow different patterns of diversification. Specifically, representatives of the *spiny leg* clade should show differentiation between islands (or volcanoes) only, whereas representatives of the web-building *elongate* clade should be capable of intra-island differentiation. This analysis required a phylogeny for each clade based on morphological characters. We marked morphological character changes and island and habitat shifts onto the

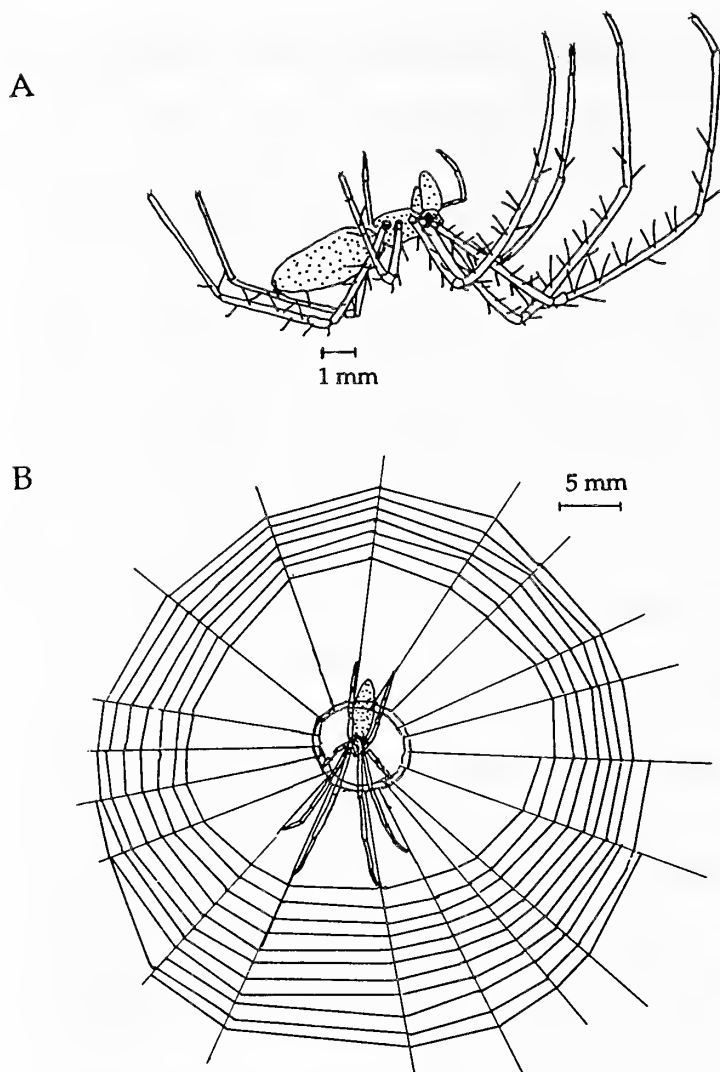


FIGURE 8.3. Hawaiian *Tetragnatha* species include web-building and non-web-building taxa. (A) Typical representative of the *spiny leg* clade (*T. waikamoi*) that has long leg spines and does not spin a web for prey capture. (B) Typical representative of the *elongate* clade (*T. stelarbusta*) that lacks the long leg spines and spins a web for prey capture.

tree to assess whether sister taxa had diverged on the same mountain masses, or only between mountain masses, and whether any ecological and associated behavioral shifts were associated with divergence.

MATERIALS AND METHODS

Choice of Outgroups

For the molecular analysis of relationships to congeners, we first used three species of *Tetragnatha* from outside the Hawaiian Islands to determine where the Hawaiian radiation fits relative to other species in the genus and also to serve as outgroups. Recent studies suggest that *T. pallescens* is very closely related to the *spiny leg* Hawaiian *Tetragnatha*, as the percent sequence difference between *T. pallescens* and *T. pilosa* is similar to the percent sequence differences among species within the *spiny leg* clade (Gillespie et al., 1994). *Tetragnatha pallescens* was therefore used as an outgroup to the Hawaiian *Tetragnatha* for the molecular

analysis. However, because we have not searched the genus exhaustively for the best outgroup to the Hawaiian *Tetragnatha*, we included two additional species in the analysis, *T. versicolor* and *T. nitens*. Each of the three non-Hawaiian species has a wide distributional range: *T. nitens* in tropical and subtropical areas worldwide; *T. pallescens* throughout North America, from Canada to Panama; and *T. versicolor* throughout the United States and southern Canada. *Tetragnatha pallescens* and *T. nitens* were collected by R.G.G. in Puerto Rico in December 1988 (*T. nitens* from Rio Camuy, *T. pallescens* from Lago de Cidra) and *T. versicolor* was collected by H.B.C. in Sewanee, Tennessee, in September 1991.

For the morphological analysis of the *spiny leg* clade, we used *Tetragnatha pallescens* as an outgroup, this species being the closest sister taxon to this clade. We also included *T. stelarobusta* in the analysis. For the *elongate* clade, molecular data suggest that *T. trituberculata*, one of the Hawaiian species, is the closest sister taxon; accordingly, it was used as an outgroup for the *elongate* clade.

Choice of Taxa for Study

We chose two groups of Hawaiian *Tetragnatha* that differ in terms of habitat associations, with the non-web-building *spiny leg* clade considered habitat generalists and the web-building *elongate* clade habitat specialists. Both molecular and morphological information suggest that the *spiny leg* clade is monophyletic; the clade is supported by one transition and one transversion in the 207-base segment of the mitochondrial DNA (mtDNA), and four nonmolecular characters (long leg spines, capture webs never built, terminal projection of conductor elongate, and considerable separation of the conductor cap from the stalk). We have insufficient information to establish the monophyly of the *elongate* clade based on molecular characters, but it is supported by four primary morphological characters (first upper cheliceral tooth very prominent, third upper cheliceral tooth bent up, lateral eyes very close together, longitudinal pattern on dorsum).

To examine phylogenetic relationships among taxa within both the *spiny leg* and the *elongate* clades, it was necessary to assign taxonomic status to the representatives of each clade. Although representatives of the *spiny leg* clade have now been described (Gillespie, 1991), those of the *elongate* clade have not yet received formal descriptions. For the purpose of the analysis, therefore, a taxonomic unit was defined as a population exhibiting a distinct set of characters unique to a given island. By this

definition, therefore, if a taxon that exhibited no detectable morphological differentiation occurred on more than one island, the population on each island was treated as a separate taxonomic unit. We included all known representatives of each clade, except for *Tetragnatha mohihi*, which appears to be in the *spiny leg* clade (Gillespie, 1991). Because we have collected only four males and no females of *T. mohihi*, we considered the information to be insufficient to use in the analysis.

Collection and Ecological Measurements

Collections of *Tetragnatha* from the Hawaiian archipelago were made at several sites in wet, mesic, and dry native forest on all the current high Hawaiian Islands. So that both island and habitat shifts could be mapped onto the phylogeny of the different clades, each habitat from which spiders were taken was scored as wet (more than 450 cm average annual rainfall), mesic (250 to 450 cm average annual rainfall), or dry (less than 250 cm average annual rainfall). Elevation was also categorized as low (less than 1,000 m), middle (1,000 to 2,000 m), or high (more than 2,000 m). Microhabitat associations were determined by categorizing the specific site from which an individual was collected (e.g., roots, fern fronds, against bark).

Phylogenetic Analysis

We used a cladistic approach (Hennig, 1966) based on both molecular (mtDNA) and morphological characters. Molecular characters were used to determine the basic clade structure of the Hawaiian *Tetragnatha* species and their relationship to several representative congeners from North America. Morphological characters were used to determine the relationship among taxa within a given clade.

For the molecular study, we amplified and sequenced a 207-base segment of mtDNA coding for most of the third domain of the RNA of the 12S ribosomal subunit for 2 to 10 individuals of eight species of Hawaiian *Tetragnatha* (*T. acuta*, *T. brevignatha*, *T. eurychasma*, *T. kama-kou*, *T. pilosa*, *T. stelarobusta*, *T. tantalus*, *T. trituberculata*) and three extra-Hawaiian species (*T. nitens*, *T. pallescens*, *T. versicolor*). Methods are given in detail elsewhere (Croom et al., 1991). Sequences were aligned by eye to the published *T. mandibulata* sequence. Using *T. pallescens* as the outgroup, we conducted a phylogenetic analysis over all bases using PAUP version 3.0s (Swofford, 1991) without weighting.

For the morphological analysis, we scored 31 characters for representatives of the *spiny leg* clade (Appendixes 8.1 and 8.2) and 30 for the *elongate* clade (Appendixes 8.3 and 8.4). The characters related to chelicer armature (upper and lower tooth rows), leg spination, color of the cephalothorax and abdomen, and structure of the male palp. Characters were analyzed as unordered states (i.e., any character state permitted to transform directly into any other state) using Fitch (Fitch, 1971) and Wagner (Farris, 1970) parsimony in PAUP (Swofford, 1991) under the accelerated transformation method of optimization. Character states were polarized as primitive or derived by outgroup comparison (Maddison et al., 1984), and characters were scaled for equal character weighting regardless of the number of states. A branch-and-bound search was conducted to find the shortest tree. The data were then reanalyzed by successive approximations, weighting characters according to their re-scaled consistency index (RC) (Farris, 1969, 1989).

Phylogenetic Relationships, Biogeography, and Habitat Association

Changes in island, volcano, and macro- and microhabitat associations were scored and marked on the morphological trees for both the *spiny leg* and *elongate* clades. In this way, we assess whether divergence was associated with colonization of volcanoes or islands, suggesting strict geographic isolation is necessary for speciation, or whether divergence was associated with ecological or behavioral shifts, suggesting the potential operation of disruptive selection driving divergence.

RESULTS

Collection and Ecological Measurements

Representatives of both *spiny leg* and *elongate* clades were found in most of the areas of native Hawaiian forest that we examined. At several sites, particularly those on Kaua'i, native *Tetragnatha* species were extremely rare. The paucity of specimens collected at several local sites on Kaua'i could be problematic for phylogenetic analysis if there was significant differentiation on a local scale. Species in the *spiny leg* clade do not appear to exhibit this level of differentiation. The *elongate* clade, however, exhibits considerable divergence on a local scale.

The island, volcano, macrohabitat, and microhabitat associations of the different species are listed in Table 8.1. Representatives of the

TABLE 8.1. Distributions and Habitats of Hawaiian *Tetragnatha*

| Taxon | Distribution | | Macrohabitat ^a | | Microhabitat | |
|------------------------|-------------------|------------------------------|---------------------------|-----------|--------------|------------|
| | Island | Volcano (if >1 on island) | Forest type | Elevation | Level | Vegetation |
| <i>spiny leg clade</i> | | | | | | |
| <i>T. pilosa</i> | Kaua'i | | Wet | Middle | Various | General |
| <i>T. restricta</i> | Maui and Hawai'i | Haleakala throughout | Various | Various | Various | General |
| <i>T. perreirai</i> | O'ahu | Wai'ananae Mts. | Wet | Middle | Various | General |
| <i>T. kamakou</i> | Moloka'i and Maui | Throughout | Wet | Various | Various | General |
| <i>T. quasimodo</i> | All except Kaua'i | Throughout five islands | Various | Various | Various | General |
| <i>T. kauaiensis</i> | Kaua'i | | Wet | Middle | Various | General |
| <i>T. waikamoi</i> | Maui | Throughout | Wet | Various | Various | General |
| <i>T. brevignatha</i> | Maui and Hawai'i | Haleakala throughout | Various | Various | Various | General |
| <i>T. tantalus</i> | O'ahu | Ko'olau Mts. | Wet | Low | Various | General |
| <i>T. macracantha</i> | Maui | Haleakala | Wet | Various | Various | General |
| <i>T. polychromata</i> | O'ahu | Wai'ananae Mts. | Wet | Low | Various | General |

elongate clade^b

| | | | | | | |
|-----------------------|----------|-----------|-----------|--------|------|-------------------|
| Elongate Kawela | Moloka'i | | Wet | Middle | Low | Grasses and ferns |
| Elongate Pihea | Kaua'i | | Wet | Middle | Low | Grasses and ferns |
| Elongate Oloku'i | Moloka'i | | Wet | Middle | Low | Open ferns |
| Elongate Lana'i | Lana'i | | Dry/mesic | Middle | Low | Open ferns |
| Elongate Waikamoi | Maui | Haleakala | Wet | Middle | Low | Open ferns |
| Laupahoe-hoe Legs | Hawai'i | Mauna Kea | Wet | | High | Trees |
| Maka'ala Legs | Hawai'i | Mauna Loa | Wet | | High | Trees |
| Elongate Ku'ia | Kaua'i | | Dry/mesic | Low | Low | <i>Styphelia</i> |
| Elongate Auwahi | Maui | Haleakala | Dry/mesic | Middle | Low | <i>Styphelia</i> |
| Elongate Kipahoe-hoe | Hawai'i | Mauna Loa | Dry/mesic | Middle | Low | Grasses |
| Elongate Laupahoe-hoe | Hawai'i | Mauna Kea | Wet | Middle | Low | Grasses |
| Elongate Mauna Kea | Hawai'i | Mauna Kea | Mesic | High | Low | <i>Sophora</i> |
| Elongate Wailuku | Hawai'i | Mauna Kea | Wet | Middle | Low | Grasses |

^aSee text for explanation of rainfall and elevational ranges.

^bThe taxa of this clade have not been formally described taxonomically and are referred to by localities in which they occur.

cursorial *spiny leg* clade tend to be distributed over broader ranges in terms of geographic distribution, forest type, and elevation and exhibit little habitat specialization. Several taxa in the *elongate* clade, however, tend to have a much more localized distribution and exhibit marked habitat specialization.

Phylogenetic Analysis

For the molecular analysis, there were 82 variable sites (Appendix 8.5). The three shortest trees generated from analysis of the 207 bases had a consistency index (CI) of 0.843, a retention index (RI) of 0.698, and an unweighted tree length of 121 (Figure 8.4 shows the strict consensus tree). The results support the monophyly of the Hawaiian *Tetragnatha* used for this part of the study. However, among the three taxa we examined from outside the Hawaiian Islands, *T. pallescens* is the very clear sister group to the Hawaiian lineage, with *T. nitens* and *T. versicolor* being only very distantly related. Indeed, preliminary results, using additional endemic species from the Hawaiian Islands and various continents, are suggesting that *T. pallescens* may fall within the Hawaiian *Tetragnatha* radiation (Gillespie et al., 1994). If this result proves valid, it might suggest that the Hawaiian *Tetragnatha* species are derived from more than one colonization event.

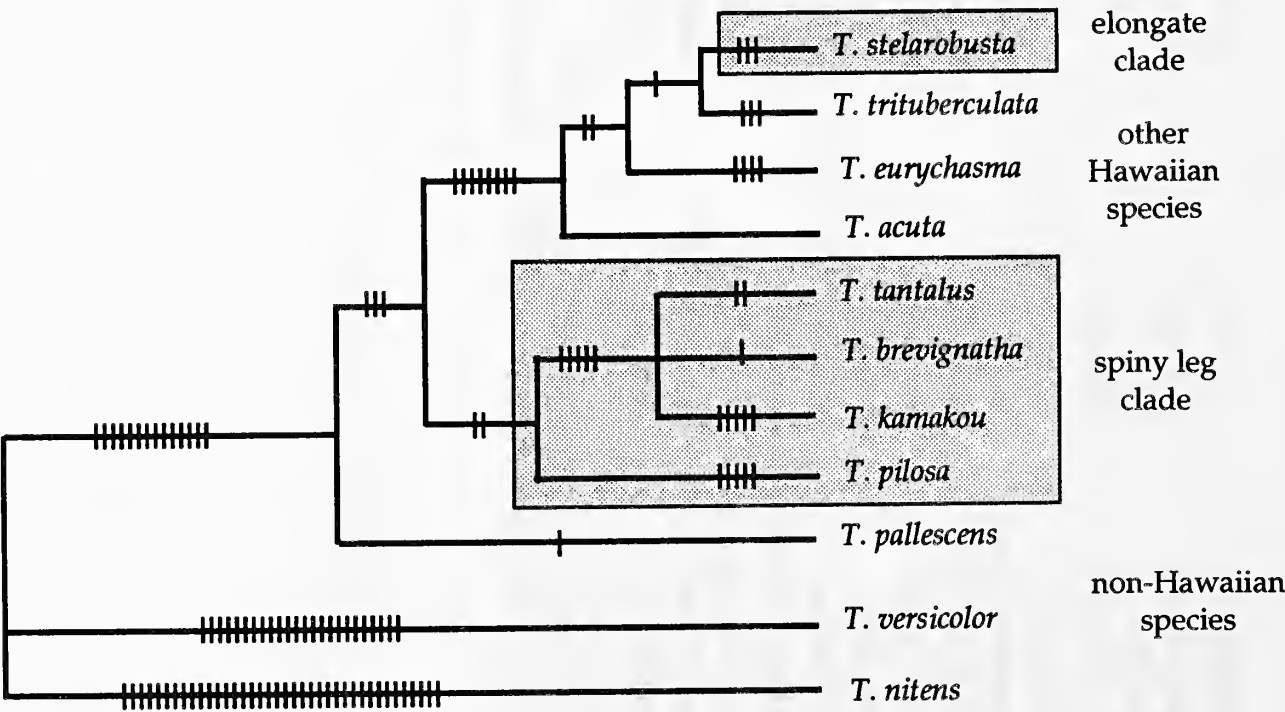


FIGURE 8.4. Phylogeny of representative Hawaiian and non-Hawaiian *Tetragnatha* based on mtDNA sequences. The number of base changes is indicated by *vertical bars*.

For both morphological analyses, characters were weighted so that they had equal weights regardless of the number of states and were unordered. The morphological analysis of the *spiny leg* clade generated four trees, which were then weighted according to the RC and re-analyzed. The result was a single tree, unweighted length 94 (CI = 0.653; RI = 0.793) (Figure 8.5). Despite the generation of the single tree, however, the topology was very vulnerable to perturbation. Deleting a single character or taxon or weighting in a different manner would change the topology radically. In particular, if the color characters (24, 25, and 27) were not included in the analysis, *Tetragnatha brevignatha* would group with *T. pilosa*, and *T. perreirai* would fall as the outgroup of *T. macracantha*, *T. quasimodo*, *T. restricta*, and *T. kamakou*. Groupings that withstood minor perturbations (and in which we therefore place more confidence) are as follows: *T. tantalus* is always sister to *T. waikamoi*; *T. polychromata* is sister to *T. macracantha*.

For the *elongate* clade, two equally parsimonious trees were generated. Subsequent weighting according to CI gave three similar trees, unweighted length 61 (CI = 0.731; RI = 0.775) (Figure 8.6 illustrates the strict consensus tree). The topology of the tree was relatively resistant to perturbation and changed little when characters or taxa were deleted.

Phylogenetic Relationships, Biogeography, and Habitat Association

As can be seen from the phylogeny of the *spiny leg* clade (Figure 8.5), the most closely related species are never found on the same island; taxa on any one island tend to be most closely related to taxa on far distant islands. This pattern is similar to that found in the *elongate* clade on the older islands but contrasts to the pattern on Hawai'i Island, where taxa in the *elongate* clade have diversified within the island (Figure 8.6).

Changes in habitat associations are marked as thick lines on the trees (Figures 8.5 and 8.6). For the *spiny leg* clade, there appears to have been one major shift in habitat association, with the bright green species (*Tetragnatha kauaiensis*, *T. tantalus*, *T. wiakamoi*, *T. polychromata*, *T. macracantha*, and *T. brevignatha*) on the left of Figure 8.5 being associated with green substrata, and the remaining taxa (on the right of the tree) associated with brown substrata. However, the branch holding these groupings together is not well supported, and it is not clear whether the habitat shift evolved once or many times. In no situation, however, are habitat shifts associated with divergence between taxa on a single island.

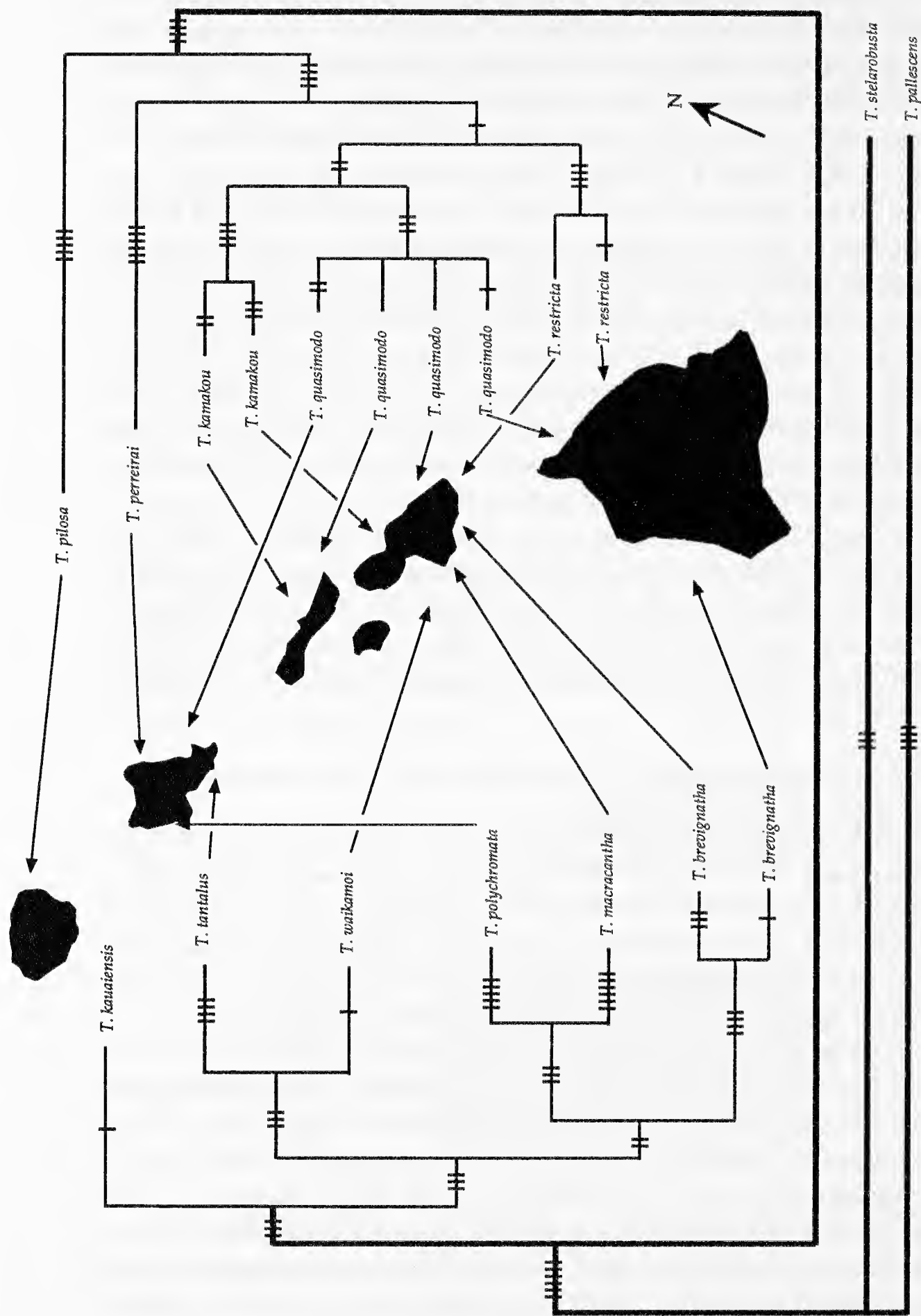


FIGURE 8.5. Phylogeny of the spiny leg clade of Hawaiian *Tetragnatha*, showing island distributions. Habitat or behavioral shifts associated with the phylogeny are indicated by wide connecting lines. Character changes are indicated by small vertical bars.

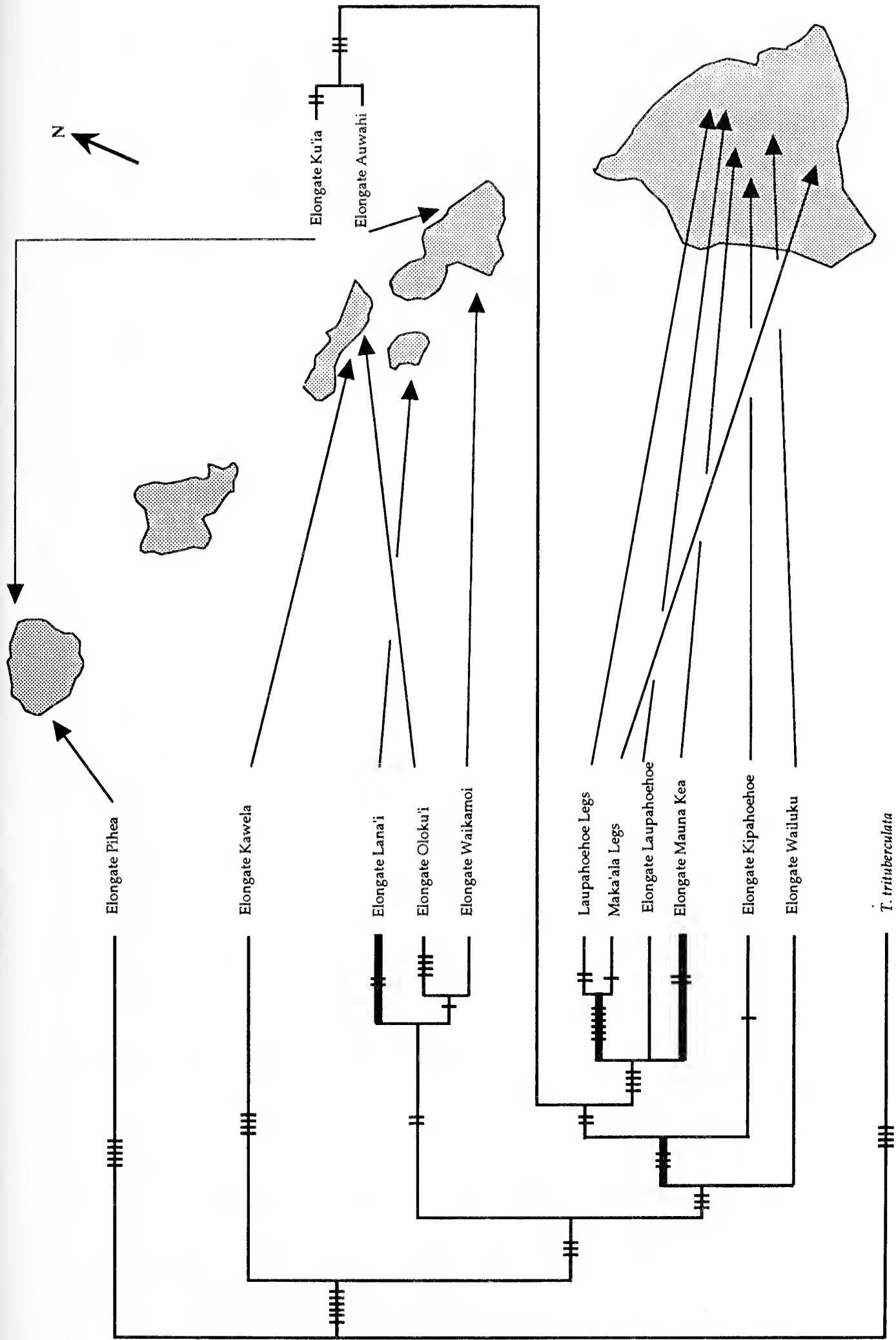


FIGURE 8.6. Phylogeny of the elongate clade of Hawaiian *Tetragnatha*, showing island distributions. Habitat or behavioral shifts associated with the phylogeny are indicated by wide connecting lines on the cladogram. Character changes are indicated by small vertical bars.

In the *elongate* clade, divergence appears to have occurred both between (older islands) and within (Hawai'i Island) volcanoes and is frequently associated with ecological and associated behavioral shifts (Figure 8.6). Such shifts are most noticeable on Hawai'i Island and are associated with development of greatly elongated tarsal claws and occupation of a higher level in the forest understory (*Tetragnatha* sp. "Laupahoehoe Legs" and *Tetragnatha* sp. "Maka'ala Legs") as well as a shift into dry forest (*Tetragnatha* sp. "Elongate Kipahoehoe" and the two sister taxa that are found on Kaua'i and Maui) and high-elevation shrubland dominated by *Styphelia* (Epacridaceae) and *Sophora* (Fabaceae) (*Tetragnatha* sp. "Elongate Mauna Kea"). Representatives from the Maui Nui complex (Maui, Moloka'i, and Lana'i) are similar (excluding *Tetragnatha* sp. "Elongate Kawela" from Moloka'i and *Tetragnatha* sp. "Elongate Auwahi" from Maui) and may represent geographic isolates of the same taxon. It appears that "Elongate Auwahi" and "Elongate Ku'ia" have arisen through back-colonization from Hawai'i to the older islands.

DISCUSSION

Divergence between species of the *spiny leg* clade of Hawaiian *Tetragnatha* appears never to have occurred on the same volcano (Figure 8.7A). In no situation are two sister species on the same volcano or even on the same island. This phylogeny therefore strongly suggests allopatric speciation between islands only. Inter-island colonization is also considered to underlie speciation in the Hawaiian *Drosophila* (Carson and Templeton, 1984). It appears that the species colonize in a generally older-to-younger island direction, with the most derived species usually found on the youngest island, Hawai'i. However, the Hawaiian *Drosophila* species generally exhibit single-volcano endemism, one species having its closest relatives on an adjacent volcano. In contrast, the *spiny leg* species of Hawaiian *Tetragnatha* exhibit a nonuniform and disjunct pattern. Also, colonization of a new habitat is clearly associated with ecological release (expansion of range and habitat use), as evidenced by the very broad ranges occupied by all *spiny leg* taxa on the youngest island (Gillespie, 1993). We suggest that, unlike the Hawaiian *Drosophila* in which sexual selection has been implicated in the speciation process (Kaneshiro, 1983; Kaneshiro and Giddings, 1987), ecological factors (range expansion, reinvasion, competition) may be more important among the *spiny leg* species of Hawaiian *Tetragnatha* (R. G. Gillespie, unpubl.).

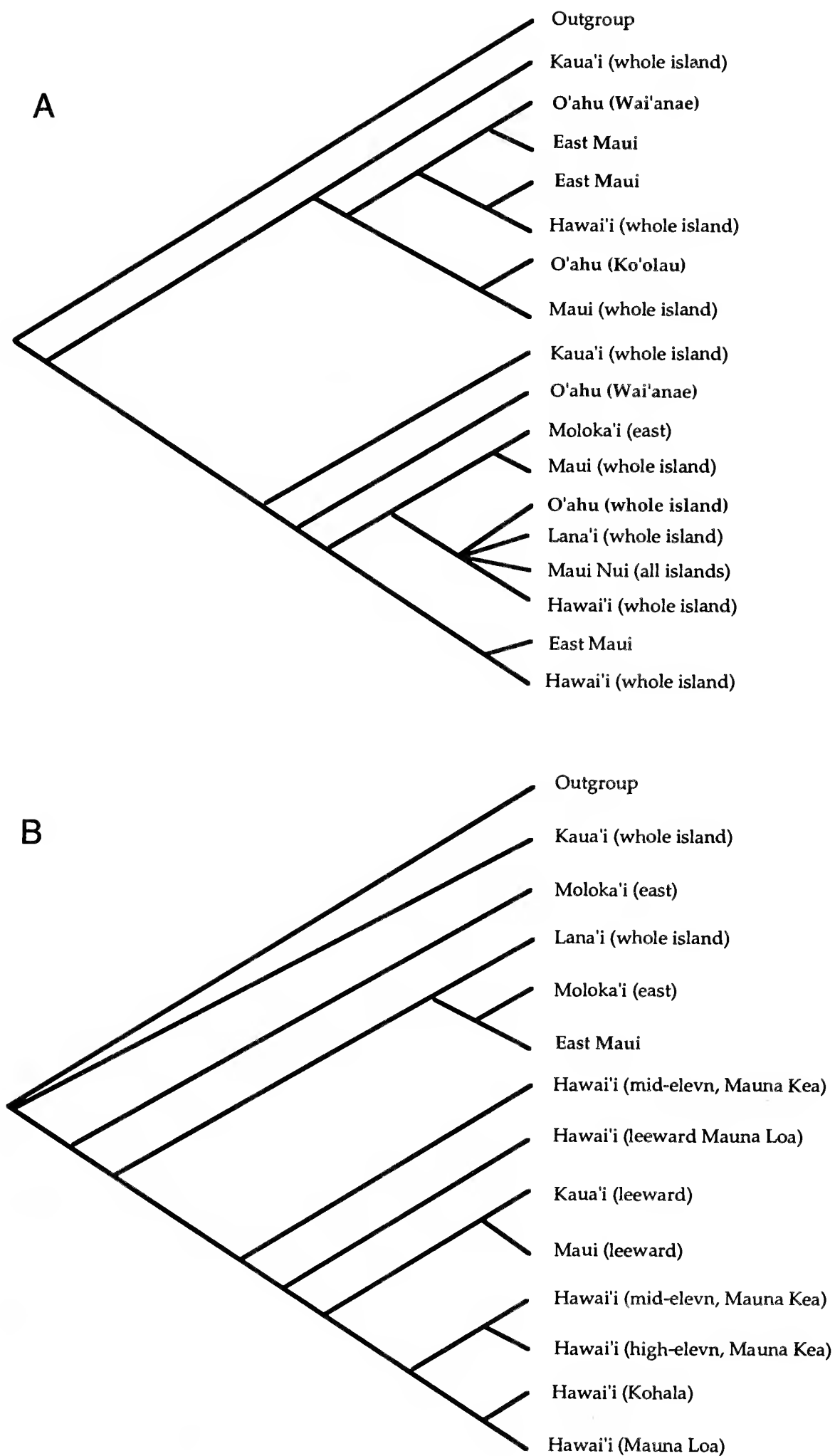


FIGURE 8.7. General area cladograms showing pattern of phylogeny of Hawaiian *Tetragnatha* relative to islands. (A) Area cladogram for *spiny leg* clade; (B) area cladogram for *elongate* clade.

The deeper nodes in the *spiny leg* phylogeny are sensitive to changes in the number of characters and taxa used, making relationships among groups of taxa more difficult to ascertain. This instability suggests the possibility that hybridization may have occurred between certain taxa, and species that tend to move around the tree (such as *Tetragnatha brevignatha*) may be of hybrid origin (Funk, 1985). We are currently examining the existence of hybridization and its importance in the evolution of the Hawaiian *Tetragnatha* (R. G. Gillespie et al., unpubl.).

As for the *spiny leg* clade, representatives of the *elongate* clade of Hawaiian *Tetragnatha* appear to have colonized islands from older to younger islands (with the exception of *Tetragnatha* sp. "Elongate Auwahi" and *Tetragnatha* sp. "Elongate Ku'ia") (Figure 8.6). However, the biogeographic pattern of phylogeny generated for the *elongate* clade contrasts with that of the *spiny leg* clade. In particular, it appears that differentiation between taxa of the *elongate* clade can occur within an island (and perhaps on a single volcano), as sister taxa are found in broadly contiguous habitats on the same land mass on Hawai'i Island (Figure 8.7B). The different pattern of phylogeny in this clade may arise partly from their web-building habit. Based on current theories, groups that are only loosely associated with habitat types, such as the Hawaiian *Drosophila* and the cursorial *spiny leg* clade of Hawaiian *Tetragnatha*, may require considerable geographic isolation to initiate divergence (Mayr, 1963; Bush and Howard, 1986; Carson, 1986). However, groups composed of taxa with more rigorous ecological associations could potentially diverge in contiguous habitats, through the action of forces such as disruptive selection (Rausher, 1984; Rosenzweig, 1990). Spiders that build webs tend to demonstrate stronger habitat affinities than cursorial species (Table 8.1) and consequently may be capable of differentiating within a single volcano. Similar patterns may be found in other Hawaiian taxonomic lineages that demonstrate habitat specialization, such as carabid beetles (J. K. Liebherr, unpubl.).

Consider the role of ecological and behavioral shifts in driving differentiation within Hawai'i Island. Representatives of the *elongate* clade examined came from a wide range of elevations and forest types (Table 8.1), but most came from broadly contiguous habitats on the flanks of the two major mountain masses on the island, Mauna Kea and Mauna Loa. One major ecological shift is the shift of *Tetragnatha* sp. "Kipahoe" from wet to dry forest. It appears that *Tetragnatha* sp. "Elongate Ku'ia" and *Tetragnatha* sp. "Elongate Auwahi" (both dry-forest

taxa) may have arisen subsequent to this ecological shift from a common ancestor with *Tetragnatha* sp. "Elongate Kipahoe." "

The most strikingly morphologically deviant taxa are *Tetragnatha* sp. "Laupahoe Legs" and *Tetragnatha* sp. "Maka'ala Legs," again from Hawai'i Island. These taxa have all developed remarkable elongation of the tarsal claws, a phenomenon that appears to have arisen independently in three quite unrelated lineages of spiders worldwide: the Gradungulidae (Forster et al., 1987); *Hetrogriffus* in the family Thomisidae (Platnick, 1976); and to a lesser extent, *Celaenia* in the Araneidae (Forster and Gray, 1979). Even in the Hawaiian Islands, however, elongation of the tarsal claws appears to have evolved independently in the *elongate* clade as well as in the extraordinary *Doryonychus raptor* (Tetragnathidae) (Gillespie, 1992b,c). *Doryonychus raptor* has abandoned web-building (Gillespie et al., 1994) and uses the tarsal claws for impaling prey. It is presently unknown whether the long-clawed representatives of the *elongate* clade have adopted a similar foraging strategy. However, unlike *D. raptor*, they appear still to be capable of web-building, as evidenced by the presence of aggregate gland spigots (in addition to flagelliforms) on their posterior lateral spinnerets, which exude the sticky silk of orb webs (R. G. Gillespie, unpubl.).

Ecological differentiation within an island does not appear to have occurred among all representatives of the *elongate* clade of Hawaiian *Tetragnatha*. The taxa from Moloka'i, Lana'i, and Maui, for example, are very similar and may represent isolated populations of a widely distributed species. The *elongate* clade does not appear to occur on O'ahu, although superficially similar representatives are found in all native forests that have been studied on the island (R. G. Gillespie, unpubl.).

The results from this study suggest that habitat associations, as indicated by web-building versus non-web-building taxa in a lineage of Hawaiian spiders, may play a role in dictating the level at which differentiation and divergence can occur within a lineage (i.e., within, or only between, islands). Habitat association does not, however, necessitate any one mode of differentiation. The non-web-building taxa, which have only very loose associations with their habitat, appear to require wide geographic dispersion to diverge and appear never to diverge on the basis of ecological or behavioral shifts. The web-building taxa, with their stronger habitat associations, appear to diverge in both geographic and ecological space, and it is the interplay of these two factors that produces the final pattern of phylogeny.

ACKNOWLEDGMENTS

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APPENDIX 8.1. Character List for *spiny leg* Clade of Hawaiian *Tetragnatha*

Female Chelicerae

1. First tooth size: 0 = pimple; 1 = small tooth; 2 = as large as others.

Male Chelicerae

2. First tooth: 0 = absent; 1 = bump; 2 = finger.
3. "sl" (1st tooth down margin): 0 = bent up; 1 = straight; 2 = bent down.
4. "sl" proximity to "T" (2nd tooth down margin): 0 = approximately contiguous; 1 = distant.
5. Apical tooth (lower chelicerae): 0 = present; 1 = absent.
6. Number of large teeth on bottom margin: 0 = 1; 1 = 2.
7. Lower tooth row: 0 = short; 1 = long.
8. Teeth 3 and 4 on lower margin: 0 = much smaller; 1 = same size as others.
9. Size of teeth 5 onwards, compared with 3 and 4: 0 = larger; 1 = smaller.
10. First two teeth: 0 = contiguous; 1 = well separated.

Male Palpal Conductor

11. Curl on terminal projection: 0 = none; 1 = slight; 2 = complete curl.
12. Terminal projection: 0 = straight; 1 = backward; 2 = forward.
13. Cap: 0 = shallow; 1 = deep.
14. Cap ridge: 0 = lateral; 1 = medial.
15. Level of backward projection compared with cap: 0 = above; 1 = at same level; 2 = below.
16. Spur of tip: 0 = indistinct; 1 = prominent.
17. Spur of tip: 0 = angled up; 1 = straight out; 2 = hooked down.
18. Floor and spur base of tip: 0 = at same level; 1 = separated.
19. Separation of cap and conductor pleats: 0 = large; 1 = small.

- 20. Cap: 0 = wide; 1 = medium; 2 = high.
- 21. Cap: 0 = rounded; 1 = pointed right; 2 = flat.
- 22. Tip: 0 = not twisted; 1 = twisted to show underside.
- 23. Tip of male conductor projection: 0 = blunt; 1 = pointed.

Color and Pattern

- 24. Venter color: 0 = translucent; 1 = dark.
- 25. Venter pattern: 0 = plain; 1 = median bar; 2 = paired spots.
- 26. Sternum color: 0 = translucent; 1 = opaque.
- 27. Dorsum color: 0 = brown; 1 = variable brown/green; 2 = green.

Feeding Behavior

- 28. Orb capture webs: 0 = built; 1 = not built.

Female Genitalia

- 29. Seminal receptacles: 0 = no swelling; 1 = swelling angled down; 2 = swelling angled up.

Leg Spination

- 30. Tibial spines leg I (lateral,medial,dorsal): 0 = 3,3,2; 1 = 4,4,2; 2 = 5,5,2.
- 31. Tibial spines leg I: 0 = short; 1 = long.

APPENDIX 8.2. Data Matrix of Morphological Character States of the *spiny leg* Clade of Hawaiian *Tetragnatha*

The characters and character states are defined in Appendix 8.1. For species with populations on more than a single island, island names are given. Missing data are indicated by a question mark.

| Species | Character | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|-------------------------------|-----------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | | |
| <i>I. kauaiensis</i> | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 1 |
| <i>I. pilosa</i> | 1 | 2 | 1 | 0 | 0 | ? | 0 | ? | ? | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | |
| <i>I. macracantha</i> | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | |
| <i>I. polychromata</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | |
| <i>I. tantalus</i> | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | |
| <i>I. waikamoi</i> | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | |
| <i>I. brevignatha</i> Maui | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | |
| <i>I. brevignatha</i> Hawai'i | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 2 | 1 | 1 | |
| <i>I. perreirai</i> | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | |
| <i>I. kamakou</i> Moloka'i | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | |
| <i>I. kamakou</i> Maui | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | |
| <i>I. restricta</i> Maui | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | |
| <i>I. restricta</i> Hawai'i | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 2 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | |
| <i>I. quasimodo</i> O'ahu | ? | 2 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | |
| <i>I. quasimodo</i> Lana'i | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | |
| <i>I. quasimodo</i> Maui | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | |
| <i>I. quasimodo</i> Hawai'i | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | |
| <i>I. stelarobusta</i> | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | ? | ? | 0 | |
| <i>I. pallescens</i> | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | 0 | |

APPENDIX 8.3. Character List for *elongate* Clade of Hawaiian *Tetragnatha*

Male Chelicerae

1. Backward projection of chelicerae: 0 = curved; 1 = bulged.
2. Fang: 0 = uniformly curved; 1 = bent.
3. Dorsal spur of chelicerae: 0 = tip pointed; 1 = tip with equal bifurcation; 2 = tip with unequal bifurcation; 3 = tip blunt.
4. First upper cheliceral tooth shape: 0 = nipple; 1 = finger; 2 = wave.
5. Second upper cheliceral tooth shape: 0 = straight; 1 = convex; 2 = concave.
6. Teeth 2 to 4 on the lower cheliceral margin: 0 = same size; 1 = smaller.
7. Teeth 2 to 4 on the lower cheliceral margin: 0 = separated; 1 = clustered.
8. Third upper cheliceral tooth: 0 = straight; 1 = curved up.
9. Cheliceral length: 0 = shorter than cephalothorax; 1 = same length as cephalothorax.
10. Dorsal spur of chelicerae: 0 = squat; 1 = medium length.

Male Cephalothorax

11. Cephalothorax: 0 = elongate; 1 = stocky.
12. Posterior median eyes relative to cephalothorax: 0 = small; 1 = large.

Male Palpal Conductor

13. Backward projection of tip: 0 = absent; 1 = present.
14. Shape of tip projection: 0 = straight; 1 = turned; 2 = curled.
15. Nipple of tip: 0 = absent; 1 = present.
16. Shape of distal section: 0 = oval; 1 = rounded; 2 = peaked.
17. Overall shape of conductor: 0 = triangular; 1 = moon; 3 = dome.

Leg Spination and Claws

18. Spines on dorsal tibia I: 0 = 1; 1 = 2.
19. Spines on medial tibia I: 0 = 0; 1 = 3.
20. Spines on lateral tibia III: 0 = 0–1; 1 = 2.
21. Spines on lateral metatarsus III: 0 = 1; 1 = 2.
22. Length leg I: 0 = < 10× length of cephalothorax; 1 = > 10× length of cephalothorax.
23. Tarsal claws: 0 = short and equal length; 1 = long and unequal length.

Female Chelicerae and Cephalothorax

24. Overall shape of cephalothorax: 0 = squat; 1 = oval; 2 = elongate.

- 25. Apical tooth on chelicerae: 0 = absent; 1 = present.
- 26. Lateral eyes: 0 = abut; 1 = close together; 2 = well separated.

Color and Pattern

- 27. Pattern on dorsum: 0 = paired spots; 1 = lines; 3 = folium.
- 28. Central sternum: 0 = pale; 1 = dark.
- 29. Dark border to sternum: 0 = absent; 1 = narrow; 2 = wide.
- 30. Legs: 0 = spotted; 1 = banded.

APPENDIX 8.4. Data Matrix of Morphological Character States of the *elongate* Clade of Hawaiian *Tetragnatha*

The characters and character states are defined in Appendix 8.3. Missing data are indicated by a question mark.

| Taxon | Character | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|----------------------|-----------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | | | |
| | | | | | | | | | | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | |
| Elongate Ku`ia | 1 | 0 | 3 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | |
| Elongate Auwahi | 1 | 0 | 3 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | ? | ? | ? | ? | ? | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | |
| Elongate Kawela | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | |
| Elongate Oloku`i | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | |
| Elongate Pihea | 0 | 0 | 2 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | ? | ? | 0 | 0 | ? | 1 | 0 | 0 | 0 | 0 | |
| Elongate Lana`i | 0 | 0 | 3 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | ? | ? | 0 | 0 | ? | 0 | 1 | 1 | 1 | 1 | |
| Elongate Waikamoi | 0 | 0 | 3 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | ? | ? | ? | ? | ? | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | |
| Elongate Kipahoehoe | 0 | 0 | 3 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 2 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | |
| Elongate Wailuku | 0 | 0 | 3 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 2 | 0 |
| Elongate Mauna Kea | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | 0 | 0 | ? | 2 | 1 | 0 | 2 | 0 | |
| Elongate Laupahoehoe | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 1 | 1 | ? | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | ? | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | |
| Maka`ala Legs | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | ? | 1 | 0 | 1 | ? | 0 | 3 | 0 | 0 | 0 | |
| Laupahoehoe Legs | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | ? | ? | ? | ? | ? | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | |
| T. trituberculata | 0 | 0 | 3 | 0 | 0 | ? | ? | 0 | 1 | 1 | 1 | 0 | ? | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | ? | 1 | 0 | 1 | |

APPENDIX 8.5. Molecular Characters Used to Determine Basic Clade Structure of Hawaiian *Tetragnatha* and Relationship to Representative Continental Congeners

Asterisks mark deletions or gaps in the DNA sequence; X, no data.

| Species | Base sequence (extended below) | | | | | | | | | | | | | | | |
|--------------------------|--------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| <u>I. stelarobusta</u> | CA | C*T | TTT | AAT | TAT | ATT | TTA | TAT | ACC | GCC | GTC | T** | TGA | ATA | GAT | CAT |
| <u>I. trituberculata</u> | .. | ... | ... | .. | ... | ... | ... | ... | ... | ... | ... | ... | .. | ... | ... | ... |
| <u>I. eurychasma</u> | .. | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | .. | ... | ... | ... |
| <u>I. acuta</u> | .. | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | .. | ... | ... | ... |
| <u>I. pilosa</u> | .. | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | .. | ... | ... | ... |
| <u>I. kanakou</u> | .. | ... | ... | .. | C | ... | ... | ... | ... | ... | ... | ... | .. | ... | ... | ... |
| <u>I. tatalus</u> | .. | .. | T | ... | ... | ... | ... | ... | ... | ... | ... | ... | .. | ... | ... | ... |
| <u>I. brevignatha</u> | .. | ... | ... | .. | T | ... | ... | ... | ... | ... | ... | ... | .. | ... | ... | ... |
| <u>I. pallescens</u> | .. | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | .. | ... | ... | ... |
| <u>I. versicolor</u> | T | ... | .. | C | .. | A | ... | ... | ... | ... | .. | T | ... | AA | ... | ATA |
| <u>I. nitens</u> | .. | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | .. | ... | ... | ... |

| Species | Base sequence (extended) |
|-------------------|---|
| I. stelarobusta | AAG *AT AAA ATG TAT TAC ACT AAA AAT TTA AGG ATC AAA TTA AAA TAT AAT *TT AAG AAA GGG GAT TTA TAA G*T ATT ATT TCA AAA TTA AAA TTt G |
| I. trituberculata | G.. ... G..T.T.A.A. |
| I. eurychasma | G..T.T. TC.A. |
| I. acuta |T.T.T. AA.T. |
| I. pilosa |T.T. G.. ... *. ... I.C. C. .T. .T. |
| I. kanakou |T.T. G.. ... *. C.. .C C.C G.. ... AA.I. .T. |
| I. tantalus | xxx xxx xxx xxx xxx xxx xxx xxx xxx xxx xxx xxx xxx xxx xxx xxx xxx xxx xxx x |
| I. brevignatha |T.T.T. G.. ... *. C.. .C T.C. AA.T. .T. |
| I. pallescens |T.T.T.T. *. A.. ... T.C C. ... AA.T. |
| I. versicolor |T. T..TCT.A ..A ..T .A. GAA T.. .AT *. ... A..T. .T. |
| I. nitens | T.. .T. T..G.T.TC T..A .AT .T A.T *.T. A.A IGAG.A. T.T. I... .A. |

9 Evolutionary Relationships of the Hawaiian Honeycreepers (Aves, Drepanidinae)

CHERYL L. TARR AND
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The effect of isolation on island faunas is often manifested by a paucity of terrestrial vertebrate lineages (Bull and Whitaker, 1975; Bloch, 1982; Simon, 1987). Among vertebrate groups, birds appear to be the most capable of colonization of isolated islands or archipelagoes (Carlquist, 1965). For example, the Hawaiian Islands harbor no native terrestrial amphibians or reptiles, and the endemic mammals are represented solely by bats (the Hawaiian hoary bat *Lasiurus cinereus semotus* and one extinct bat) (James et al., 1987). In contrast, at least 20 natural avian colonizations have been suggested (James, 1991). Thus, with one exception, birds are the only group of terrestrial vertebrates known to have successfully colonized the isolated Hawaiian archipelago.

Despite its predominance, the Hawaiian avifauna is a depauperate group (Freed et al., 1987). In the case of songbirds, only 6 (James and Olson, 1991) of 84 extant passerine families (Clements, 1991) are represented in the Hawaiian Islands. As with other groups of organisms in the Hawaiian Islands (e.g., insects, plants, snails), the diversity of the avifauna has been secondarily enriched through speciation within the archipelago (Simon, 1987). Although virtually all the avian lineages have diversified, only the Hawaiian honeycreepers, or Hawaiian finches (Drepanidinae), have undergone an extensive adaptive radiation. Estimates of the number of species known historically range from 29 (Pratt et al., 1987) to 33 (James and Olson, 1991). One taxonomic treatment (Pratt, 1979) divides these into three tribes: the Drepanidini ("red" birds);

the Psittirostrini ("finch-billed" birds); and the Hemignathini ("green" birds). Representatives of each of these three tribes are illustrated in Figure 9.1. In addition to the 33 species known historically, another 14 honeycreeper species have recently been described from subfossil remains (James and Olson, 1991); this number will likely increase, as some drepanidine fossils are too fragmentary for diagnosis.

Unfortunately, of the species known historically, at least 10 Hawaiian honeycreepers are now extinct and many of the remaining species are endangered. Although the full reconstruction of the evolutionary history of the honeycreepers will require consideration of the distribution and relationships of all taxa, both extant and extinct, molecular studies, which can include extinct taxa, have only recently become feasible. Thus, the reconstruction of evolutionary relationships presented here is only a partial one, because only a few rare and no extinct drepanidines are included. Nucleotide sequence analyses of mitochondrial DNA (mtDNA) from many of the extinct taxa are under way (R. C. Fleischer et al., unpubl.). Also, our analyses provide mitochondrial gene trees; such gene trees may differ from the actual phylogeny among closely related organisms (Tateno et al., 1982; Pamilo and Nei, 1988; Avise, 1989).

Here we compare phylogenetic relationships inferred from restriction fragment analyses of mtDNA with those derived from morphological (Amadon, 1950; Raikow, 1977; Pratt, 1979) and other biochemical (Johnson et al., 1989) characters. We refer primarily to Pratt's (1979, 1992a,b) investigations because of the relative thoroughness of his analyses. Also, we overlay the distributions of the taxa onto the phylogeny and speculate about the patterns of colonization and processes of adaptive radiation.

MATERIALS AND METHODS

Laboratory Methodology

The sample size and distribution for each taxon used in this study is given in Table 9.1. A modification of the sucrose gradient protocol described by Spolsky and Uzzell (1984) was used to isolate mtDNA. For each reaction, approximately 20 ng of mtDNA was digested with one of the following 17 restriction endonucleases (all of which recognize a unique six-base-pair sequence, except *StyI*, which recognizes a five-base-pair sequence): *BamHI*, *BanIII*, *BclI*, *BglI*, *BglII*, *BstBI*, *EcoRI*, *EcoT22I*, *HindIII*, *KpnI*, *NdeI*, *PstI*, *SacII*, *Sall*, *StyI*, *XbaI*, and *XhoI*. Fragments were fill-in

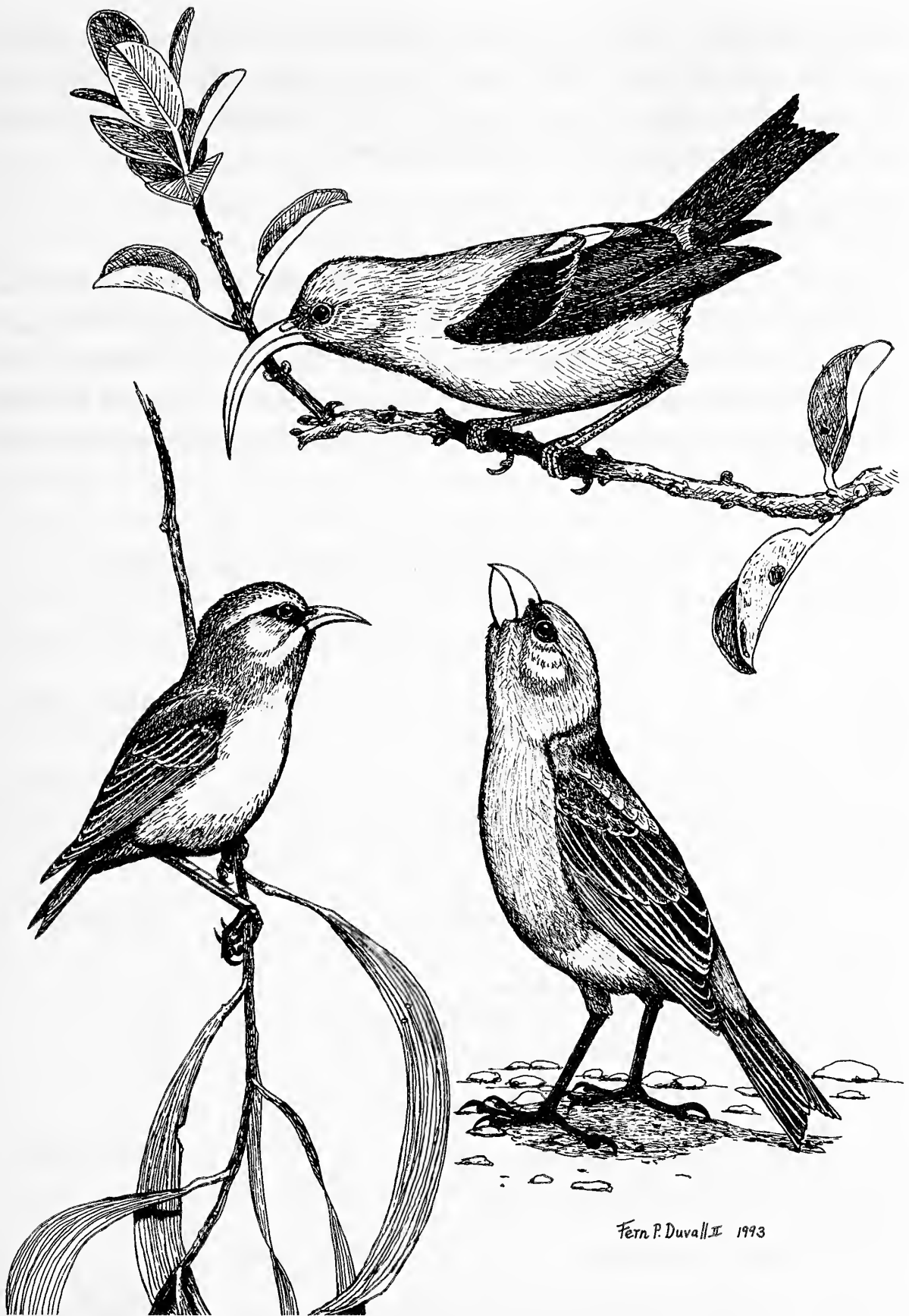


FIGURE 9.1. Three major lineages of Hawaiian honeycreepers are represented by the 'I'iwi (top, *Vestiaria coccinea* in the Drepanidini), the 'amakihi (lower left, *Hemignathus virens* in the Hemignathini), and the Laysan Finch (lower right, *Telespiza cantans* in the Psittirostrini).

end-labeled with $^{32}\text{PdNTPs}$ and electrophoresed in 1.0 to 1.5% agarose gels. After the gels were dried under vacuum, fragments were visualized by autoradiography. Autoradiographs were scored, and a presence/absence matrix of fragments was constructed.

Data Analysis

Parsimony analysis was performed by PAUP (Swofford, 1991); an heuristic algorithm (TBE branch swapping) was used on the complete fragment matrix (all 25 individuals of 13 taxa) (see Table 9.1). A branch-and-bound algorithm also was used on a subset of the data, which included two outgroup individuals of the House Finch (*Carpodacus mexicanus*)

TABLE 9.1. Sample Size and Distribution of Each Taxon Analyzed in This Study

| Taxon ^a | No. in sample | Distribution ^b |
|---|---------------|---------------------------|
| Cardueline outgroup | | |
| <i>Carpodacus mexicanus</i> (House Finch) | 2 | North America |
| Psittirostrini ("finch-billed" taxa) | | |
| <i>Telespiza cantans</i> (Laysan Finch) | 3 | La (O, Mo) |
| Incertae sedis | | |
| <i>Paroreomyza montana</i> (Maui Creeper) | 2 | M (Mo, L) |
| Hemignathini ("green" birds) | | |
| <i>Oreomystis bairdi</i> (Kaua'i Creeper) | 1 | K |
| <i>Loxops caeruleirostris</i> ('Akeke'e; Kaua'i 'Akepa) | 1 | K |
| <i>Loxops coccineus coccineus</i> (Hawai'i 'Akepa) | 3 | H |
| <i>Hemignathus parvus</i> ('Anianiau) | 2 | K |
| <i>H. virens stejnegeri</i> (Kaua'i 'Amakihi) | 1 | K |
| <i>H. virens wilsoni</i> (Maui 'Amakihi) | 1 | *Mo, M (L) |
| <i>H. virens virens</i> (Hawai'i 'Amakihi) | 1 | H |
| Drepanidini ("red" birds) | | |
| <i>Vestiaria coccinea</i> ('I'iwi) | 3 | K, *O, *Mo, M (L) |
| <i>Himatione sanguinea sanguinea</i> ('Apapane) | 3 | K, *O, *Mo, M, *L, H |
| <i>Palmeria dolei</i> ('Akohekohe) | 2 | M (Mo) |

^aTribe assignment follows Pratt (1979).

^bIslands are represented as follows: La, Laysan; K, Kaua'i; O, O'ahu; Mo, Moloka'i; M, Maui; L, Lana'i; H, Hawai'i. Former ranges (Scott et al., 1986; James and Olson, 1991) are in parentheses. *, extant populations not sampled.

and one individual of each of the honeycreeper taxa. A cardueline finch was selected as the outgroup on the basis of morphological (Sushkin, 1929; Bock, 1960; Raikow, 1977; Pratt, 1979) and DNA-DNA hybridization (Sibley and Ahlquist, 1982) results, which indicate that the carduelines are the sister group to the Drepanidinae. We also conducted an heuristic search for all trees 350 steps or less and constructed a 50% majority rule consensus of these trees.

Swofford and Olsen (1990) have cautioned against the use of restriction fragment data in parsimony analyses because characters are not independent of each other. Therefore, rather than conducting additional parsimony analyses (i.e., a bootstrap), we assessed the consistency of our phylogram by a distance analysis. A matrix of pairwise distances was calculated from the fragment data with the program RESTSITE (Miller, 1990). A tree was constructed from this matrix by a neighbor-joining algorithm (Saitou and Nei, 1987) in the analysis package MEGA (Molecular Evolutionary Genetics Analysis) (Kumar et al., 1993).

RESULTS

The honeycreeper mtDNA molecule is approximately 17,252 base pairs (bp) ± 173 bp in size; there was no significant difference in the size of the

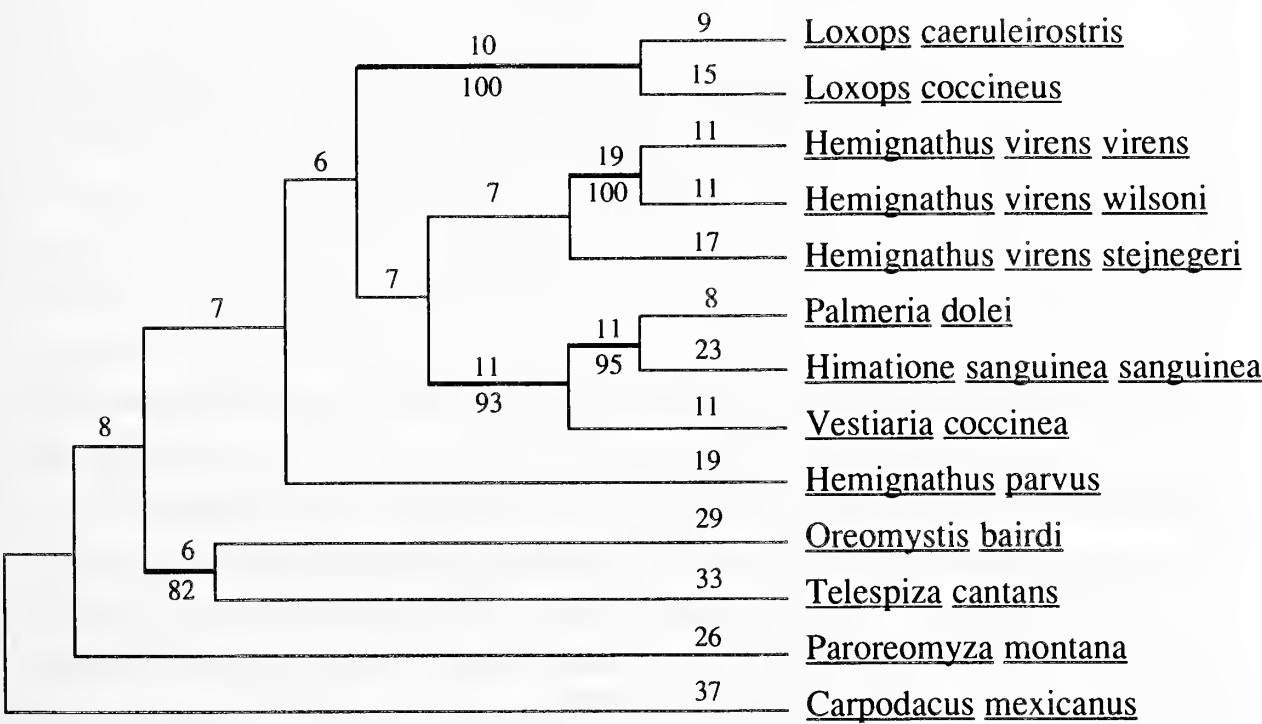


FIGURE 9.2. Single most-parsimonious cladogram produced by PAUP. Numbers along branches indicate the number of steps that occur along that branch. Total tree length is 341 steps (consistency index = 0.598).

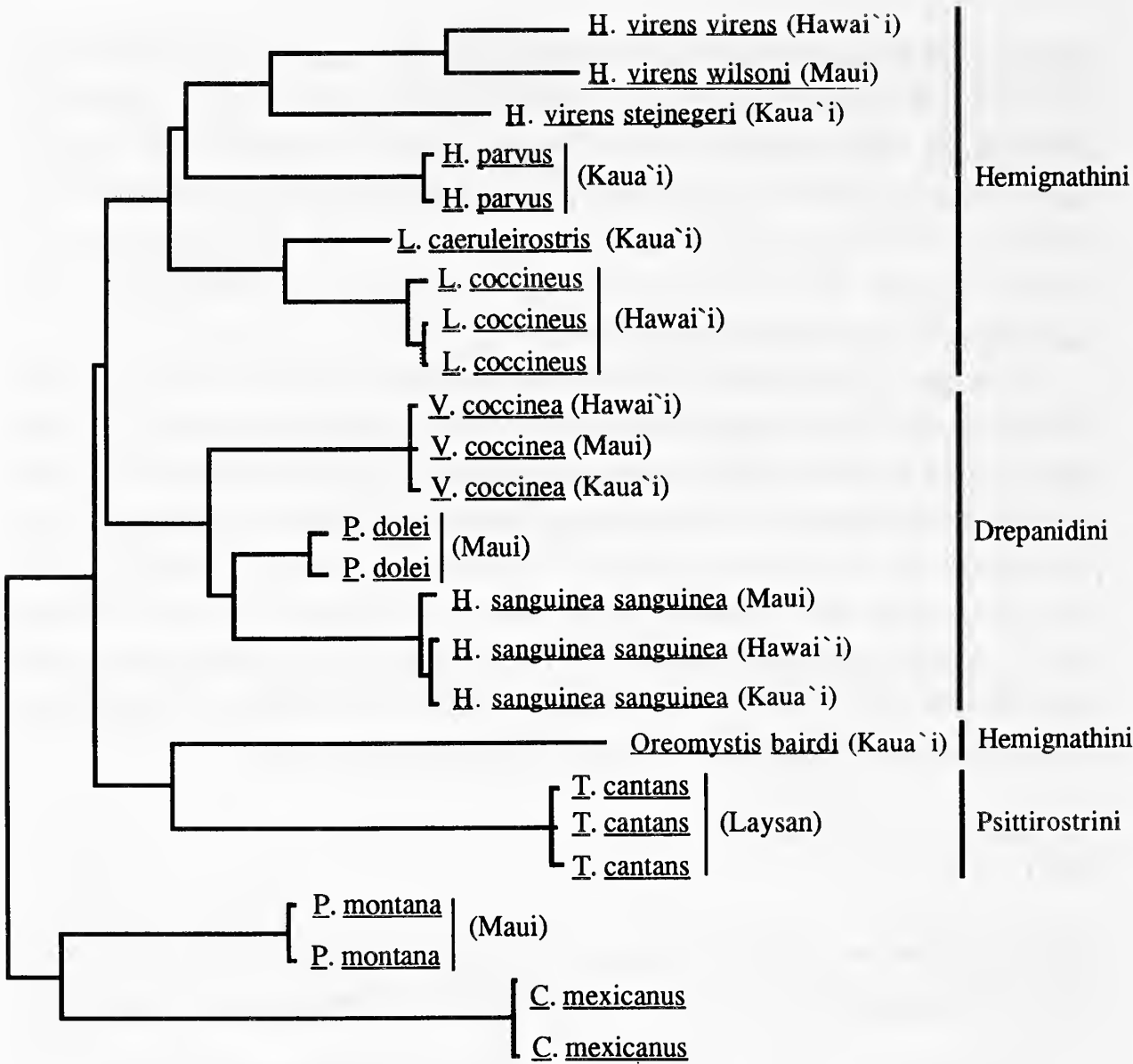


FIGURE 9.3. Neighbor-joining tree constructed from distances calculated by the method of Nei and Miller (1990) for *Hemignathus virens*, *H. parvus*, *Loxops*, *Vestiaria*, *Palmeria dolei*, *Himatione sanguinea*, *Telespiza*, and *Paroreamyza montana* using *Carpodacus mexicanus* as the outgroup. All 25 individuals (Table 9.1) were included in the analysis.

molecule among the six drepanidine taxa nor was the size of the mtDNA molecule in *Carpodacus mexicanus* (17,056 bp \pm 260 bp) significantly different from honeycreeper mtDNA. The restriction digestions produced 209 fragments. The distances calculated between all pairs of taxa are shown in Appendix 9.1. The mean estimated genetic distance among the drepanidine taxa was 0.042; the average distance between the outgroup species and the honeycreepers was 0.068.

Both the heuristic and branch-and-bound algorithms produced a single most-parsimonious tree; these trees were 346 and 341 steps, respectively. The topology of the tree resulting from the branch-and-bound

algorithm is shown in Figure 9.2. The nodes resolved in a 50% majority rule consensus of all 443 trees 350 steps or less are indicated in Figure 9.2. Single-taxon clades (e.g., *Telespiza cantans*, *Loxops coccineus*) were present in all 443 trees. All interior branches except the five stable branches (bold in Figure 9.2) collapse in a consensus of 20 trees of length 347 or less.

The tree produced by the neighbor-joining algorithm (Figure 9.3) differs from the parsimony tree in the position of three lineages: It places the 'akepa (*Loxops*) species and the 'Anianiau (*Hemignathus parvus*) within the same cluster as the 'amakihi; and the Maui Creeper (*Paroreomyza montana*) is grouped with the House Finch (*Carpodacus mexicanus*).

DISCUSSION

Relationships of the Drepanidinae

Many of the groupings within our trees coincide with traditional taxonomic divisions. For example, the 'akepa species form a clade in the parsimony tree, as do the red birds along with *Hemignathus virens*. However, the tribe Hemignathini and the genus *Hemignathus* are paraphyletic in the cladogram. The neighbor-joining tree is more consistent with the morphology-based classification; the Drepanidini and Hemignathini are both monophyletic (with the exception of *Oreomystis bairdi*; but see below). The placement of the Kaua'i Creeper (*O. bairdi*) and the Laysan Finch (*Telespiza cantans*) as sister taxa in both trees suggests that, of the taxa included in the analyses, *O. bairdi* is the closest relative of the finch-billed group (but this does not mean it is the closest relative of *T. cantans*). Our results indicate that the split between *Oreomystis* and the psittirostrine taxa occurred early in honeycreeper evolution.

Although the relationship between *Oreomystis bairdi* and *Telespiza cantans* was initially surprising, Pratt (1992b) recently suggested a similar scenario on the basis of morphological traits. In association with nectarivory, many honeycreepers have a tubular tongue and a well-developed nasal operculum (Amadon, 1950; Raikow, 1977). Neither structure is present in *Oreomystis* or in the psittirostrine taxa (with the exception of *Psittirostra psittacea*—a species we were unable to include in our analyses because of its rarity—which possesses a moderately developed

nasal operculum) (Raikow, 1977). Although Pratt (1979) originally inferred a secondary loss of both the nasal operculum and the tubular tongue by placing *O. bairdi* as a sister taxon to the 'akepa, 'amakihi, and red birds, he recently suggested a closer relationship between *Oreomystis* and the Psittirostrini (Pratt, 1992b), thereby providing a more parsimonious reconstruction for the evolution of these two characters.

The placement of *Oreomystis bairdi* with a thick-billed species—rather than with other small-billed species such as *Hemignathus parvus* and the 'akepa—suggests that either small-billed insectivorous forms have arisen independently at least twice from a thick-billed finch ancestor or the founding species was a small-billed species of finch (e.g., similar to the Pine Siskin, *Carduelis pinus*). Our results are consistent with the hypothesis of Perkins (1903), who proposed that the main lineages of drepanidines arose independently from a generalized, small-billed ancestor.

Many of the interior nodes of our parsimony trees are not well supported. Thus, we do not address the polarity of change of other character states during honeycreeper evolution. Although the limitations of restriction fragment analysis may be in part responsible for the lack of resolution, we hypothesize that the initial radiation of major lineages occurred very rapidly; recovering the initial branching order could prove difficult, regardless of the type of data used to reconstruct a phylogeny. Preliminary analysis of mitochondrial cytochrome *b* sequence suggests a similar rapid radiation of major lineages (R. C. Fleischer et al., unpubl.).

The relationship of *Paroreomyza montana* to the Drepanidinae remains uncertain. The inclusion of only one outgroup in the parsimony analysis does not allow us to address the question of monophyly with a cladistic analysis; the neighbor-joining tree supports a monophyletic origin for the honeycreepers, with the exception of *P. montana*, which clusters with *Carpodacus mexicanus* outside the drepanidines. Our results are thus consistent with Pratt's (1979, 1992b) hypothesis for *Paroreomyza*. Although several studies have concluded that the honeycreepers (including *P. montana*) are monophyletic (e.g., Raikow, 1977; Johnson et al., 1989; James and Olson, 1991), Pratt has argued that the characters on which the inclusion of *Paroreomyza* (and *Melamprosops*, the *Po'ouli*) is based are plesiomorphic. Pratt (1992a,b) maintained that the unique odor (initially noted by Perkins, 1903) and the proximally truncate tongue (or lack of "lingual wings") of drepanidines are the only synapomorphies that unite the group—and these two synapomorphies are lacking in *Melamprosops* and *Paroreomyza*. Although it cannot be ruled out that *Paroreomyza* and *Melamprosops* diverged before the development of the

odor and loss of lingual wings, Pratt (1992a,b) concluded that, because they do not share synapomorphies with other drepanidines, these two taxa may represent independent (possibly cardueline) colonizations.

The exclusion of *Paroreomyza montana* from the other drepanidines by the neighbor-joining analysis is suggestive. However, we cannot yet rule out the possibility that the rate of substitution is decelerated in *P. montana* relative to the other drepanidine lineages (as branch lengths suggest); if this is so, then the average distance from the other honeycreepers to *P. montana* could be longer than the distance from the outgroup to *P. montana*. Neighbor-joining trees can be rooted at the midpoint along the branch between the operational taxonomic units (OTUs) separated by the largest distance. Thus, this rooting could result in an apparent clustering of *P. montana* and *Carpodacus mexicanus*. We believe that it would be premature to exclude *P. montana* from the honeycreepers on the basis of our results; a cladistic analysis with more outgroup taxa may provide an unambiguous placement of the root of the drepanidine tree. We suggest that if *P. montana* is a honeycreeper, then it represents a lineage that diverged soon after the initial colonization.

Time Frame for Honeycreeper Evolution

The small average genetic distance among honeycreeper taxa is striking, given the extensive morphological diversity exhibited among the species included here. The average d_{xy} for honeycreepers (0.042) is comparable to the average intrageneric divergence in several continental taxa (Table 9.2) and is less than the divergence between two populations of a New World tropical species, *Saltator albicollis* ($d_{xy} = 0.063$) (Seutin et al., 1993). The close genetic relationship among the Drepanidinae suggests that the morphological diversification of honeycreeper taxa occurred rapidly on the main islands (Kaua'i to Hawai'i).

The small distance between *Carpodacus mexicanus* and the Drepanidinae also supports a rapid origin of honeycreeper diversity. Assuming a constant molecular clock with a rate of about 2% divergence per million years—the rate obtained by a calibration in one honeycreeper lineage (Tarr and Fleischer, 1993) and proposed for geese (Shields and Wilson, 1987)—the initial arrival of a drepanidine ancestor occurred approximately 3.5 million years ago. A few caveats accompany the time estimate. *Carpodacus mexicanus* is not necessarily the cardueline most closely related to the honeycreepers, and there are large stochastic errors associated with estimating divergence times from molecular data (Hillis

TABLE 9.2. Average Interspecific Divergence of mtDNA in Avian Genera

| Genus | No. of species compared | No. of individuals | d_{xy} | Reference |
|--------------------|-------------------------------|-----------------------|----------|----------------------------|
| <i>Quiscalus</i> | 4 | 13 | 0.033 | Zink et al., 1991b |
| <i>Zonotrichia</i> | 5 | 22 | 0.041 | Zink et al., 1991a |
| <i>Dendroica</i> | 5 | 11 | 0.044 | Kessler and Avise, 1985 |
| <i>Platycercus</i> | 6 | 26 | 0.046 | Ovenden et al., 1987 |
| <i>Anas</i> | 9 | 24 | 0.062 | Kessler and Avise, 1985 |
| <i>Pipilo</i> | 6 | 27 | 0.064 | Zink and Dittman, 1991 |

and Moritz, 1990). Previous studies have suggested divergence times of 15 to 20 million years (Sibley and Ahlquist, 1982) to 7 to 8 million years (Johnson et al., 1989). Our rough estimate corresponds more closely with that of Johnson et al. (1989); we suggest a relatively recent arrival for the honeycreeper ancestor.

Biogeography

In general, our results are consistent with one biogeographic pattern commonly seen in other groups of Hawaiian organisms, a relationship between cladogram order and island age. For example, in both the parsimony and neighbor-joining tree, *Oreomystis bairdi*, a species endemic to Kaua'i, is derived earlier within the honeycreeper clade. Also, *Hemignathus parvus*, another Kaua'i endemic, is a basal taxon in the parsimony analysis and is basal to the 'amakihi species in the neighbor-joining tree. Last, *Hemignathus virens stejnegeri*, the Kaua'i 'Amakihi, is the oldest of the three 'amakihi lineages included here (however, in an earlier study, which included the O'ahu 'Amakihi, *H. virens chloris*, we could not resolve which taxon, *H. virens stejnegeri* or *H. virens chloris*, was derived earlier) (Tarr and Fleischer, 1993). None of these Kaua'i taxa have been found as fossils on other islands (James and Olson, 1991).

A second biogeographic pattern often seen in Hawaiian organisms is the presence of sister taxa on the same island. Such a pattern might not

be expected here given the high vagility of avian taxa and their relative lack of habitat specialization compared with invertebrates and plants. Thus far, we do not have evidence for sympatric speciation in the honeycreepers (however, with the addition of extinct taxa to the phylogeny, different patterns may be detected). On the contrary, in lineages that are widespread and differentiated (e.g., 'amakihi and 'akepa species), sister taxa are found on different islands. In these lineages, diversification appears to be a consequence of inter-island dispersal and isolation.

In contrast, two of the Drepanidini taxa show that inter-island dispersal may not always lead to divergence among populations: The highly nectarivorous 'Apapane (*Himatione sanguinea sanguinea*) and 'Iiwi (*Vestiaria coccinea*) are widespread, but neither has differentiated morphologically (Berger, 1981; Freed et al., 1987) or genetically (Appendix 9.1; C. L. Tarr et al., unpubl.; Johnson et al., 1989) within or among the main islands (but see below). The 'O'u (*Psittirostra psittacea*), for which we do not have genetic data, shows a similar morphological pattern (Freed et al., 1987).

The lack of inter-island differentiation and intra-island variation in *Himatione sanguinea sanguinea* and *Vestiaria coccinea* may be a result of recent range expansion and/or high gene flow among islands; the pattern of genetic variation does not allow us to differentiate between these two processes, but both are plausible. Pratt (1979) proposed that both species expanded their ranges in response to the arrival and spread of 'ohi'a (*Metrosideros polymorpha* Gaud.), which may have occurred relatively recently. It has also been suggested that the extinction of other avian taxa may have allowed the expansion of these two species. Although gene flow among islands has not been documented, long-distance intra-island movements have been observed for both *Himatione* and *Vestiaria* (Baldwin, 1953; MacMillen and Carpenter, 1980). Also, flocks of *H. sanguinea sanguinea* have reportedly been carried to neighboring islands by high winds, even as far as Laysan Island (Munro, 1960). However, the establishment of breeding individuals is confirmed only on Laysan, where colonization gave rise to a subspecies of the 'Apapane (*H. sanguinea freethi*, now extinct). The intra-island movements of these two taxa are apparently in response to regional flowering of 'ohi'a (MacMillen and Carpenter, 1980); the spatial and temporal availability of nectar resources may have selected for the habit of high, long-distance flights in the two species, and inter-island dispersal could occur as a consequence of such flight patterns.

SUMMARY

The morphological diversity of the Hawaiian honeycreepers appears to be the result of a recent and rapid adaptive radiation; genetic differentiation between species is less than would be expected on the basis of morphological divergence. Given the estimated arrival date of this group and the distribution of basal taxa, we suggest Kaua'i as the source of initial colonization of the other high islands.

Speciation in some honeycreepers appears to follow an allopatric model. However, differentiation has not occurred in all widespread taxa; *Himatione sanguinea sanguinea* and *Vestiaria coccinea* have likely expanded their range recently, possibly in response to ecological changes. Inter-island gene flow may be occurring, but this has not been documented. *Himatione sanguinea sanguinea* and *V. coccinea* may instead represent the early stage of a new cycle of dispersal and differentiation, as suggested by Pratt (1979).

Although the variety in many groups of Hawaiian organisms may have been diminished by extinction, the loss of diversity of the avifauna in historical and prehistorical times has been well documented. Recent developments in molecular biology allow the use of subfossils (Cooper et al., 1992) and study-skin material (Pääbo, 1989) in molecular systematic analyses. We have begun similar analyses of extinct taxa to investigate evolutionary patterns more fully in the honeycreepers. For example, because human colonization so severely affected the psittirostrine taxa (James, 1991), the evolution of this diverse lineage remains to be explored.

ACKNOWLEDGMENTS

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APPENDIX 9.1.1. Estimates of mtDNA Divergence (d_{xy}) between Honeycreeper Taxa (Above Diagonal) with Standard Errors (Below Diagonal)

Values shown here have been multiplied by 100. For taxa with sample size of more than one individual, within-taxon differences are shown on the diagonal (in boldface). In column headings and row headings, the numbers represent the following taxa: (1) *Loxops caeruleirostris*; (2) *Loxops coccineus*; (3) *Oreomystis bairdi*; (4) *Paroreomyza montana*; (5) *Hemignathus parvus*; (6) *Hemignathus virens stejnegeri*; (7) *H. virens wilsoni*; (8) *H. virens virens*; (9) *Palmeria dolei*; (10) *Himatione sanguinea sanguinea*; (11) *Vestiaria coccinea*; (12) *Telespiza cantans*; (13) *Carpodacus mexicanus*.

| Taxon | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|-------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| 1 | — | 1.73 | 5.59 | 4.46 | 3.09 | 3.80 | 4.35 | 4.42 | 3.69 | 4.17 | 3.88 | 5.44 | 6.79 |
| 2 | 0.68 | — | 6.09 | 4.87 | 3.70 | 4.31 | 5.12 | 5.48 | 3.84 | 4.81 | 3.89 | 4.99 | 6.77 |
| 3 | 1.15 | 1.23 | — | 6.24 | 5.70 | 8.28 | 6.75 | 6.03 | 4.84 | 6.19 | 6.41 | 5.84 | 7.51 |
| 4 | 0.96 | 0.93 | 1.40 | 0.00 | 4.64 | 6.99 | 5.95 | 6.40 | 4.46 | 4.57 | 5.67 | 5.53 | 5.21 |
| 5 | 0.97 | 1.06 | 1.19 | 0.91 | 0.00 | 3.27 | 5.08 | 5.47 | 4.19 | 5.54 | 4.77 | 6.39 | 5.88 |
| 6 | 1.06 | 1.21 | 1.16 | 1.26 | 0.94 | — | 3.96 | 3.53 | 4.42 | 5.69 | 3.76 | 6.26 | 5.71 |
| 7 | 0.94 | 0.82 | 1.40 | 1.23 | 1.01 | 0.71 | — | 1.80 | 5.99 | 6.98 | 5.69 | 7.02 | 5.77 |
| 8 | 0.86 | 0.64 | 1.23 | 1.16 | 0.91 | 0.94 | 0.67 | — | 5.70 | 6.25 | 5.40 | 5.52 | 7.26 |
| 9 | 0.89 | 0.88 | 1.05 | 0.97 | 1.41 | 1.35 | 1.20 | 1.12 | 0.06 | 2.28 | 2.10 | 4.59 | 5.76 |
| 10 | 0.93 | 0.99 | 1.25 | 1.07 | 1.67 | 1.54 | 1.39 | 1.27 | 0.80 | 0.11 | 3.49 | 5.19 | 6.79 |
| 11 | 1.12 | 1.05 | 1.26 | 1.18 | 1.53 | 1.22 | 1.38 | 1.08 | 0.59 | 0.79 | 0.00 | 5.52 | 6.49 |
| 12 | 1.02 | 1.04 | 1.80 | 0.79 | 1.53 | 1.27 | 1.08 | 1.42 | 1.39 | 1.19 | 1.29 | 0.00 | 10.6 |
| 13 | 1.49 | 1.21 | 1.65 | 1.09 | 1.48 | 1.54 | 1.16 | 1.38 | 0.97 | 1.56 | 1.54 | 2.33 | 0.00 |

10 Biogeography of Seven Ancient Hawaiian Plant Lineages

V. A. FUNK AND WARREN L. WAGNER

There are 32 endemic flowering plant genera in the Hawaiian Islands and more than 200 endemic flowering plant lineages (Wagner et al., 1990). These diversified Hawaiian plants have long been a focus of research on adaptive radiation, speciation, dispersal, and biogeography (Carlquist, 1974, 1980, 1981; Carson and Templeton, 1984; Carson, 1987a). However, no one has used phylogenetic methods to search for repeating patterns in these endemic lineages. Moreover, there has been little use of phylogenetic hypotheses to investigate issues such as biogeography and speciation. In this chapter, we compare the evolution of seven individual lineages with the geologic evolution of the Hawaiian Islands. We then use the patterns produced to discuss colonization and speciation in these groups.

Seven unrelated endemic lineages were selected to determine whether common patterns occur (Table 10.1). They consist of five genera, one section of a genus, and two genera that together form a single lineage, for a total of eight genera. Two of the genera, *Wilkesia* and *Argyroxiphium*, are discussed also by Baldwin and Robichaux in this volume (Chapter 13). The selected lineages met several criteria. Most important, each one had to be demonstrably monophyletic and endemic to the Hawaiian Islands and to consist of three or more species. Another criterion was that each selected lineage had to occur on multiple islands of the archipelago but the species of the lineage, insofar as possible, should be restricted to a single island. This would allow biogeographic comparisons within the

archipelago but simplify the problems of interpretation of widespread species distributions. Whenever possible, the outgroup taxon (taxa) was extra-Hawaiian. Because all seven lineages selected were morphologically distinctive and clearly monophyletic, it was thought that they were, therefore, more likely to be of ancient origin than lineages whose members are similar to those from other geographic areas. Such ancient lineages presumably have a better chance of having a history influenced by the geologic development of the archipelago.

When possible, data for the groups studied were confirmed from specimens in the U.S. National Herbarium, Smithsonian Institution, and the herbarium at the Bishop Museum. Field work was conducted by the authors in 1991 and 1992 to check the consistency of certain characters. Species studied in the field had been well collected at the study sites or are thought to be nearly extinct. Therefore, data collection was based on observations and photographs and only rarely documented by voucher specimens.

MATERIALS AND METHODS

Eight genera comprising seven lineages from four families were studied (Table 10.1; Figure 10.1). Data matrices and character lists are given for all analyses. All the known autapomorphic characters as well as potential synapomorphic characters were included in the analysis because, although the synapomorphic characters indicate the relationships among the species, the autapomorphic ones are useful in determining the amount of morphological change in the individual species. For all the lineages studied, the last one or two transformation series in each data matrix are the distribution and/or the habitat. These transformation series were excluded from the analysis and were never used to construct the phylogenies.

In this study, the term *transformation series* (TS) is used to indicate a grouping of two or more characters that are believed to be homologous. Each transformation series is, therefore, a statement of homology made by the authors. Transformation series are often called "characters" by other authors, and characters are referred to as "character states."

The data were analyzed using PAUP version 3.1.1 (Swofford, 1993) and MacClade 3.01 (Maddison and Maddison, 1992). All characters were unordered. ACCTRAN and DELTRAN options were used and gave uniform results. All indexes were calculated using PAUP and ignoring the uninformative characters. When a species had more than one character

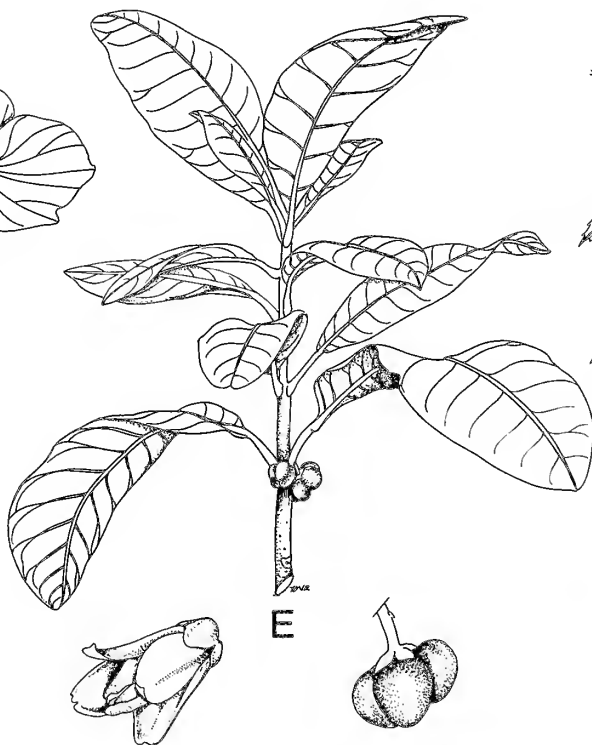
TABLE 10.1. Selected Endemic Hawaiian Plant Genera Used in Phylogenetic and Geographic Analyses

| Taxon | Distribution | Elevational range (m) | Habitat |
|---|--|-----------------------|--|
| Asteraceae, Heliantheae, | | | |
| Madiinae | | | |
| <i>Argyroxiphium caliginis</i> C. Forbes | West Maui | 1,350–1,650 | Bog |
| <i>A. grayanum</i> (Hillebr.) Degener | West and East Maui | 1,200–2,050 | Bog perimeter, wet forest |
| <i>A. kauense</i> (Rock & M. Neal) Degener & I. Degener | Mauna Loa and Hualalai, Hawai'i | 1,625–1,900 | Bog to wet forest |
| <i>A. sandwicense</i> DC subsp. <i>macrocephalum</i> (A. Gray) Meyrat | East Maui | 2,125–3,050 | Alpine desert |
| <i>A. sandwicense</i> DC subsp. <i>sandwicense</i> | Mauna Kea, Hawai'i | 2,700–3,750 | Alpine desert |
| <i>A. virescens</i> Hillebr. | East Maui | 1,600–2,300 | Mesic to wet forest |
| <i>Wilkesia gymnoxiphium</i> A. Gray | Kaua'i | 425–1,100 | Dry to mesic forest |
| <i>W. hobdyi</i> St. John | Kaua'i | 275–400 | Dry ridges |
| Asteraceae, Astereae | | | |
| <i>Remya kauaiensis</i> Hillebr. | Kaua'i | 1,050 | Mesic forest |
| <i>R. mauiensis</i> Hillebr. | West Maui | 850–920 | Mesic forest |
| <i>R. montgomeryi</i> W. L. Wagner & Herbst | Kaua'i | 1,030 | Cliffs, mesic forest remnant |
| Asteraceae, Mutisieae, Cochnatiinae | | | |
| <i>Hesperomannia arborescens</i> A. Gray | Ko'olau Mts., O'ahu; Moloka'i, Lana'i, and West Maui | 360–750 | Slopes and ridges, wet forest |
| <i>H. arbuscula</i> Hillebr. | Wai'anae Mts., O'ahu; West Maui | 350–900 | Slopes and ridges, mesic to wet forest |
| <i>H. lydgatei</i> C. Forbes | Kaua'i | 600–750 | Wet forest |
| Geraniaceae | | | |
| <i>Geranium arboreum</i> A. Gray | East Maui | 1,520–2,150 | Subalpine shrubland |
| <i>G. cuneatum</i> Hook. | Hawai'i | 1,480–3,050 | Subalpine shrubland and forest, foggy lava pioneer |
| <i>G. hanaense</i> Medeiros & St. John | East Maui | 1,670–1,680 | Bog |
| <i>G. humile</i> Hillebr. | West Maui | 1,490–1,770 | Bog |

(Continued)

TABLE 10.1. (Continued)

| Taxon | Distribution | Elevational range (m) | Habitat |
|--|--|--------------------------|---|
| <i>G. kauaiense</i> (Rock) St. John | Alaka'i Swamp to Mount Wai'ale'ale, Kaua'i | 1,220–1,250 | Bog |
| <i>G. multiflorum</i> A. Gray | East Maui | 1,580–2,450 | Montane grassland to wet forest, some- times subalpine shrubland |
| <i>G. tridens</i> Hillebr. | East Maui | 2,300–3,250 | Alpine shrubland |
| Malvaceae | | | |
| <i>Hibiscadelphus</i> sp. nov. | Kaua'i | 990–1,020 | Mesic forest remnant |
| <i>H. bombycinus</i> C. Forbes | Kohala Mts., Hawai'i | Unknown | Mesic forest |
| <i>H. crucibracteatus</i> Hobdy | Lana'i | 750 | Dry forest? |
| <i>H. distans</i> L. Bishop & Herbst | Kaua'i | 350 | Dry forest |
| <i>H. giffardianus</i> Rock | Mauna Loa, Hawai'i | 1,310 | Mesic forest |
| <i>H. hualalaiensis</i> Rock | Hualalai, Hawai'i | Unknown | Dry to mesic forest |
| <i>H. wilderianus</i> Rock | East Maui | 800 | Dry forest |
| <i>Kokia cookei</i> Degener | Moloka'i | 400 | Dry forest |
| <i>K. drynarioides</i> (Seem.) Lewton | Hualalai, Hawai'i | 460–900 | Dry forest |
| <i>K. kauaiensis</i> (Rock) Degener & I. Degener | Kaua'i | 350–660 | Mesic forest |
| <i>K. lanceolata</i> Lewton | O'ahu | Unknown | Unknown |
| Rutaceae | | | |
| <i>Platydesma cornuta</i> Hillebr. var. <i>cornuta</i> | Ko'olau Mts., O'ahu | 340–920 | Mesic forest |
| <i>P. cornuta</i> Hillebr. var. <i>decurrens</i> B. Stone | Wai'anae Mts., O'ahu | ca. 700 | Mesic forest |
| <i>P. remyi</i> (Sherff) Degener et al. | Kohala, Hawai'i | 820–1,080 | Wet forest |
| <i>P. rostrata</i> Hillebr. | Kaua'i | 760–1,220 | Mesic forest and valleys |
| <i>P. spathulata</i> (A. Gray) B. Stone | Kaua'i, O'ahu, Maui, Hawai'i | 450–1,420 | Mesic to wet forest |



for a specific transformation series, it was coded as polymorphic. Trees were drawn using the "ladderlike" progression to the right to facilitate comparison with the geology of the Hawaiian Islands. However, this does not alter the fact that the significant area hypotheses are those found at the nodes of the area cladograms after the distribution has been optimized.

RESULTS

The results from the analysis of each lineage are discussed separately. The character list, data matrix, character status list, tree length, consistency index (CI), and rescaled consistency index (RC) are given for each analysis. Also, at least two trees are provided for each analysis: a phylogram, which is a cladogram in which the branch length equals the number of characters on that branch; and an area cladogram, which is a cladogram that has the taxon name replaced by its geographic distribution.

Hibiscadelphus

Hibiscadelphus is an endemic Hawaiian genus of seven species in the Malvaceae most closely related to *Hibiscus* (Bishop and Herbst, 1973). It is easily identified as a monophyletic clade by a unique corolla that is curved and narrowly convolute with the two lower petals shorter than the others (Figure 10.1A; Appendix 10.1, TS 13 and 14). Most species of *Hibiscadelphus* (Table 10.1) are endangered or extinct. One of the endangered species is newly discovered and awaiting description (D. H. Lorence and W. L. Wagner, unpubl.). The new species lacks mature fruit, which is reflected in the data matrix (Appendix 10.2, TS 3 to 6).

Fourteen transformation series (TS) were identified with 26 potentially useful characters (Appendixes 10.1 and 10.2). TS 15 and 16 are the species geographic distributions and are included to assist in the biogeographic analysis only; they were excluded from the cladistic analysis. Sixteen of the characters proved to be informative (Table 10.2).

←

FIGURE 10.1. Representatives of six of the seven lineages analyzed. (A) *Hibiscadelphus hualalaiensis*; (B) *Remya kauaiensis*; (C) *Hesperomannia arbuscula*; (D) *Kokia kauaiensis*; (E) *Platydesma spathulata*; (F) *Geranium arboreum*. Reproduced from Wagner et al. (1990), courtesy of Bishop Museum Press, Bishop Museum, Honolulu, Hawai'i. The seventh lineage, the silversword alliance, is illustrated in Baldwin and Robichaux (this volume; see Figures 13.1, 13.3, and 13.4).

TABLE 10.2. Character Status for *Hibiscadelphus*

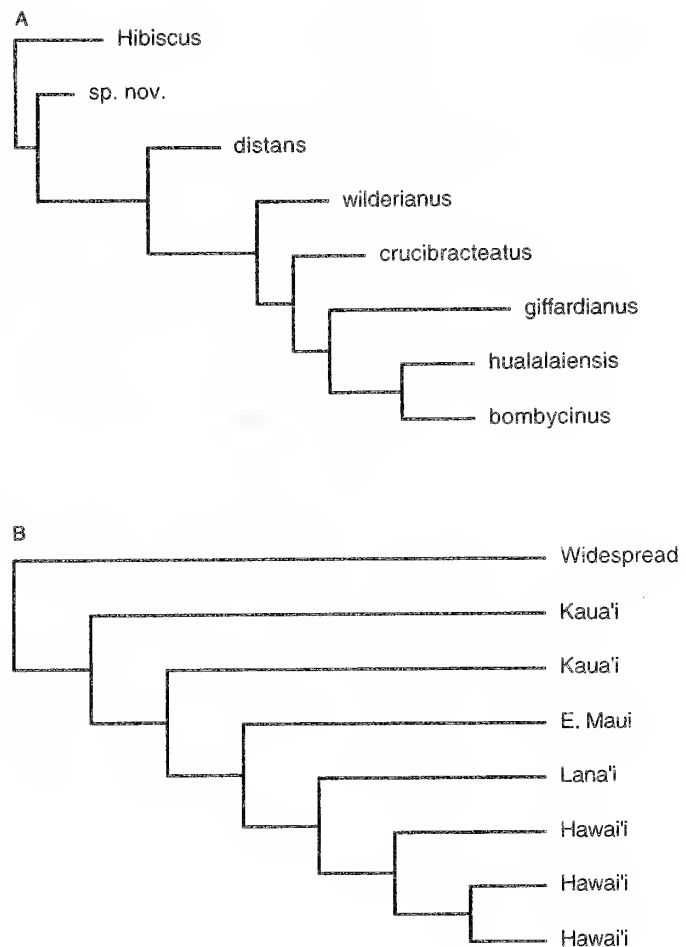
| Transformation Series ^a | Informative | Status | Characters |
|------------------------------------|-------------|----------|------------|
| 1 | Yes | Included | 012 |
| 2 | Yes | Included | 01 |
| 3 | Yes | Included | 01 |
| 4 | Yes | Included | 012 |
| 5 | No | Ignored | 0123 |
| 6 | Yes | Included | 01 |
| 7 | No | Ignored | 0123 |
| 8 | Yes | Included | 01 |
| 9 | No | Ignored | 012 |
| 10 | Yes | Included | 0123 |
| 11 | Yes | Included | 012 |
| 12 | Yes | Included | 0123 |
| 13 | No | Ignored | 01 |
| 14 | No | Ignored | 01 |
| 15 | Yes | Excluded | 01234 |
| 16 | Yes | Excluded | 0123 |

^aAll are unordered.

The sister group of *Hibiscadelphus* is *Hibiscus*; however, *Hibiscus* proved to be too variable in most characters to be useful as an outgroup for *Hibiscadelphus*. Thus, it was necessary to select some subset of *Hibiscus* as the outgroup. Unfortunately, the relationship between *Hibiscadelphus* and *Hibiscus* is not well understood, and after examining several options, two closely related, red-flowered Hawaiian species were selected as the outgroup because they have several features that are prevalent in all subgroups of the genus. The species, *Hibiscus clayi* Degener & I. Degener and *H. kokio* Hillebr., are endemic to the Hawaiian Islands (Bates, 1990).

The cladistic analysis resulted in one tree (Figure 10.2A). The length of the tree is 19, the CI is 0.842, and the RC is 0.769. The position occupied on the cladogram by the new Kaua'i species is basal. However, its placement is confounded because of the unknown fruit characters (TS 3 to 6). The PAUP analysis estimated that the fruit characters of the new species would be plesiomorphic; to investigate what would happen to the new species if the missing characters were not plesiomorphic, the taxon was recoded with the missing characters as apomorphic. This second analysis resulted in the same position on the cladogram for the new species; thus, the basal position of the new species is stable.

FIGURE 10.2. Single most-parsimonious cladogram resulting from the analysis for *Hibiscadelphus*. (A) Phylogram; (B) area cladogram.



The area cladogram (Figure 10.2B) shows the basal two species on Kaua'i, the central two on Lana'i and East Maui, and the species of the terminal clade on different volcanoes of the island of Hawai'i. When the distributions are optimized on the cladogram, the most-parsimonious arrangement shows a progression from Kaua'i to Lana'i and East Maui to Hawai'i, from the oldest of the main islands to the youngest.

The two species with the largest number of plesiomorphic characters, *Hibiscadelphus distans* and the new species, are found on Kaua'i, showing that some groups have basal species that have not accumulated large numbers of autapomorphic characters. The species with the largest number of autapomorphic characters is *H. giffardianus*, endemic to Mauna Loa on Hawai'i. Although the species of *Hibiscadelphus* are well defined, many of the internodes have only one or two synapomorphies. The exception is the internode that separates the two Kaua'i species from the clade found on the younger islands of Maui, Lana'i, and Hawai'i, which has several synapomorphic characters. This pattern of basal species occurring on the older island with a well-defined clade on the younger islands, sometimes skipping O'ahu, is not uncommon.

Remya

Remya is a Hawaiian genus of three species in the tribe Astereae (Asteraceae) that is easily distinguished by the presence of a reduced and modified pappus (see Figure 10.1B; Appendix 10.3, TS 17). *Remya* is also identifiable as a monophyletic group by its sprawling, liana-like habit and staminate inner disk florets (TS 15). All three species in the genus (see Table 10.1) have had, at least historically, a restricted distribution and are infrequently collected.

Eighteen transformation series were identified with 20 potentially useful characters (Appendixes 10.3 and 10.4). Of the 20 characters, 9 proved to be informative (Table 10.3).

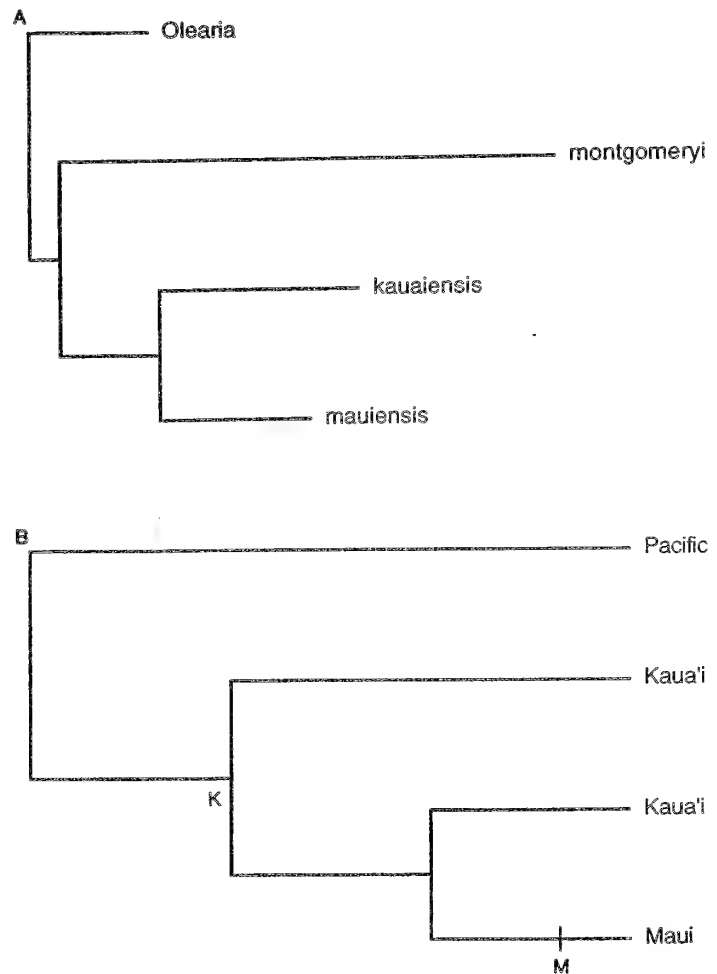
Remya is probably most closely related to the Pacific genus *Olearia*, sharing several characters with it (Wagner and Herbst, 1987; Xiaoping and Bremer, 1993). Unfortunately, there are more than 130 species of *Olearia*, and it proved impossible to determine which species of *Olearia* were most closely related to *Remya*. Also, the species of *Olearia* have many characters that are variable. This is reflected in the fact that seven

TABLE 10.3. Character Status for *Remya*

| Transformation series ^a | Informative | Status | Characters |
|------------------------------------|-------------|----------|------------|
| 1 | No | Ignored | 01 |
| 2 | Yes | Included | 01 |
| 3 | No | Ignored | 01 |
| 4 | No | Ignored | 01 |
| 5 | No | Ignored | 01 |
| 6 | Yes | Included | 01 |
| 7 | Yes | Included | 01 |
| 8 | Yes | Included | 01 |
| 9 | No | Ignored | 01 |
| 10 | Yes | Included | 012 |
| 11 | Yes | Included | 01 |
| 12 | Yes | Included | 01 |
| 13 | No | Ignored | 01 |
| 14 | No | Ignored | 012 |
| 15 | No | Ignored | 01 |
| 16 | Yes | Included | 01 |
| 17 | No | Ignored | 01 |
| 18 | No | Ignored | 012 |
| 19 | Yes | Excluded | 01 |

^aAll are unordered.

FIGURE 10.3. The one cladogram resulting from the analysis for *Remya*. (A) Phylogram; (B) area cladogram. K, Kaua'i; M, Maui.



of the transformation series used in the analysis have more than one character in *Olearia* (Appendix 10.4). This ambiguity decreased the ability of several of the characters to determine polarity.

The cladistic analysis resulted in one tree with a length of 15, a CI of 1.0, and an RC of 1.0 (Figure 10.3A). The high CI and RC are partially the result of the fact that many of the transformation series could not be polarized. In fact, a character diagnosis revealed that of the nine informative characters, only two link *Remya kauaiensis* and *R. mauiensis* and therefore provide the tree with all its structure. These two characters, stout peduncle size (TS 7) and disk floret shape (TS 16), give direction to the remainder of the potentially informative characters, all of which turn out to be autapomorphic.

Optimizing the distribution on the area cladogram (Figure 10.3B) shows that the basal species was on Kaua'i and that a subsequent dispersal event to West Maui resulted in speciation. Although consisting of only three species, *Remya* falls into the oldest-to-youngest island dispersal pattern. The species with the greatest number of apomorphic characters is *R. montgomeryi*, which is endemic to Kaua'i, the oldest island.

Hesperomannia

Hesperomannia is a genus in the tribe Mutisieae (Asteraceae) with large, yellow, discoid heads (see Figure 10.1C). The species are visited and presumed to be pollinated by birds, and it is possible that the seeds of the original colonist were bird-dispersed to the archipelago (Carlquist, 1974). In addition to the above characters, the three species of this genus (see Table 10.1) are trees with chartaceous leaves on long slender petioles (TS 18) and have a scabrous pappus (TS 17).

Eighteen transformation series were identified with 21 potentially useful characters (Appendixes 10.5 and 10.6). Of the 21 characters, 7 proved to be informative (Table 10.4).

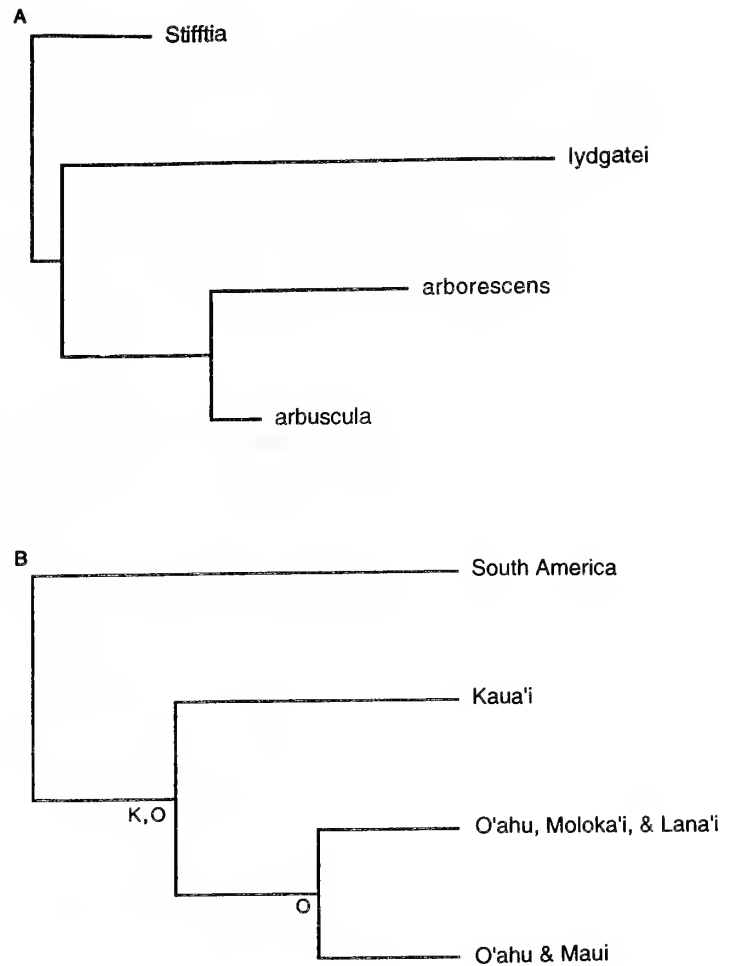
Hesperomannia has been presumed to be most closely related to *Stiffia*, a South American genus (Hillebrand, 1888). However, the characters they share are most likely plesiomorphic. Another possible sister genus is *Stenopadus*, from the Guayana area of South America. It shares several plesiomorphic characters with *Hesperomannia* and has fewer

TABLE 10.4. Character Status for *Hesperomannia*

| Transformation series ^a | Informative | Status | Characters |
|------------------------------------|-------------|----------|------------|
| 1 | No | Ignored | 01 |
| 2 | No | Ignored | 012 |
| 3 | Yes | Included | 01 |
| 4 | No | Ignored | 01 |
| 5 | Yes | Included | 01 |
| 6 | Yes | Included | 01 |
| 7 | Yes | Included | 01 |
| 8 | No | Ignored | 012 |
| 9 | No | Ignored | 012 |
| 10 | Yes | Included | 01 |
| 11 | No | Ignored | 01 |
| 12 | No | Ignored | 01 |
| 13 | Yes | Included | 01 |
| 14 | No | Ignored | 01 |
| 15 | No | Ignored | 01 |
| 16 | Yes | Included | 01 |
| 17 | No | Ignored | 01 |
| 18 | No | Ignored | 01 |
| 19 | No | Excluded | 012345 |

^aAll are unordered.

FIGURE 10.4. The one cladogram resulting from the analysis for *Hesperomannia*. (A) Phylogram; (B) area cladogram. K, Kaua'i; O, O'ahu.



apomorphic characters than *Stiffia*. However, no synapomorphic character was found to link *Hesperomannia* and either of these two genera. For this study, *Stiffia* was selected as the outgroup, but the condition of each character in *Stenopadus* was evaluated so as not to inadvertently use characters that were unique in *Stiffia*.

The cladistic analysis resulted in one cladogram with a length of 11, a CI of 1.0, and an RC of 1.0 (Figure 10.4A). This result is an example of how the CI and RC are not very useful in evaluating a cladogram. For instance, of the 21 potentially useful characters, 3 gave the cladogram all its structure (TS 10, 13, and 16), the remainder being either autapomorphic or synapomorphic for the genus. In fact, one could remove any two of these three characters and still get an RC and CI of 1.0. A similar situation occurs in *Remya*.

The area cladogram (Figure 10.4B) indicates O'ahu as the probable island where the ancestor of *Hesperomannia arborescens* and *H. arbuscula* occurred. The basal sister species of this clade occurred on Kaua'i. Although this pattern is not directional by itself, it is congruent with a pattern of colonization from an older to a younger island. This area cladogram illustrates how it is impossible to achieve a complete resolu-

tion using optimization unless there are two branches at the base of the cladogram with at least one island in common.

The species with the largest number of autapomorphic characters is *Hesperomannia lydgatei* (Figure 10.4A), endemic to Kaua'i, which agrees with Carlquist's evaluation of the derived nature of this species (1957a).

Wilkesia and *Argyroxiphium*

The species of *Wilkesia* and *Argyroxiphium* range from the tall and slender *W. gymnoxiphium* to the massive *A. sandwicense*. In fact, *A. sandwicense* is among the most striking plants of the Hawaiian Islands. The seven species of these two genera (see Figures 13.1 and 13.3; Table 10.1) are members of the tribe Heliantheae subtribe Madiinae (Asteraceae). *Wilkesia* is distinguished by whorled leaves with fused bases (TS 4) and setulose corolla tubes (TS 15) and *Argyroxiphium* by several characters including partially fused leaf bases (TS 4), ventral pappus reduction (TS 10), aristate pappus (TS 18), and two anatomical characters identified by Carlquist (1957b), the presence of pectic channels (TS 16) and leaves with few vascular bundles (TS 17).

Despite the unusual features that delimit the genera, consistent characters within species, which could be used to group species, were difficult to identify. Eventually, 18 transformation series with 24 potentially useful characters were identified (Appendixes 10.7 and 10.8), all of which were informative (Table 10.5) (Funk, 1993).

In our first analysis, *Dubautia* was used as the outgroup. *Dubautia* is also endemic to the Hawaiian Islands, and it is widely recognized that *Dubautia*, *Argyroxiphium*, and *Wilkesia*, commonly referred to as the silversword alliance, arose from a single North American colonist (Carlquist, 1959a; Carr, 1985, 1990; Baldwin et al., 1991). However, after several attempts at analyzing the data, no synapomorphy for *Dubautia* was found. *Dubautia* probably is a paraphyletic group, which agrees with the analyses by Baldwin et al. (1991) based on molecular data. Carlquist suggested that the Hawaiian silversword alliance belongs to the subtribe Madiinae, the tarweeds (Carlquist, 1959a). Recent molecular studies have shown that the Hawaiian genera are most closely related to *Madia* and *Raillardiodopsis* (see Baldwin and Robichaux, this volume, Chapter 13). For this analysis, *Dubautia* was divided into its three sections, and the genus *Madia* was added as an additional outgroup.

Using *Madia* and the three sections of *Dubautia* as the outgroups resulted in 12 equally parsimonious trees with a tree length of 34, a CI of

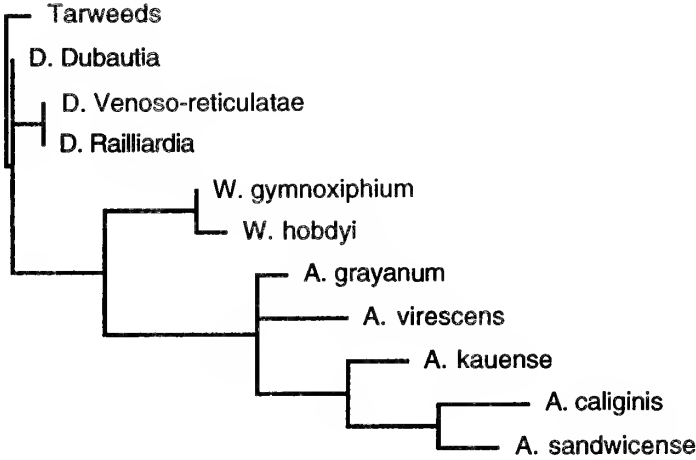
TABLE 10.5. Character Status for *Argyroxiphium* and *Wilkesia*

| Transformation series ^a | Status | Characters |
|------------------------------------|----------|------------|
| 1 | Included | 01 |
| 2 | Included | 012 |
| 3 | Included | 01 |
| 4 | Included | 012 |
| 5 | Included | 012 |
| 6 | Included | 01 |
| 7 | Included | 01 |
| 8 | Included | 01 |
| 9 | Included | 01 |
| 10 | Included | 0123 |
| 11 | Included | 01 |
| 12 | Included | 012 |
| 13 | Included | 01 |
| 14 | Included | 01 |
| 15 | Included | 01 |
| 16 | Included | 01 |
| 17 | Included | 01 |
| 18 | Included | 01 |
| 19 | Excluded | 01234 |

^aAll are unordered and informative.

0.794, and an RC of 0.652. Examination of the trees showed that nine of the trees resulted from rearrangements of the relationships among the three sections of *Dubautia* and therefore could be ignored. Only three of the equally parsimonious trees involved rearrangements of the species of *Argyroxiphium* and *Wilkesia*. A phylogram of one tree is shown in Figure 10.5. Figure 10.6 shows the three topologies and the strict consen-

FIGURE 10.5. One of the 12 equally parsimonious cladograms of the silversword alliance, drawn as a phylogram. Nine of the cladograms involve rearrangements of the out-groups.



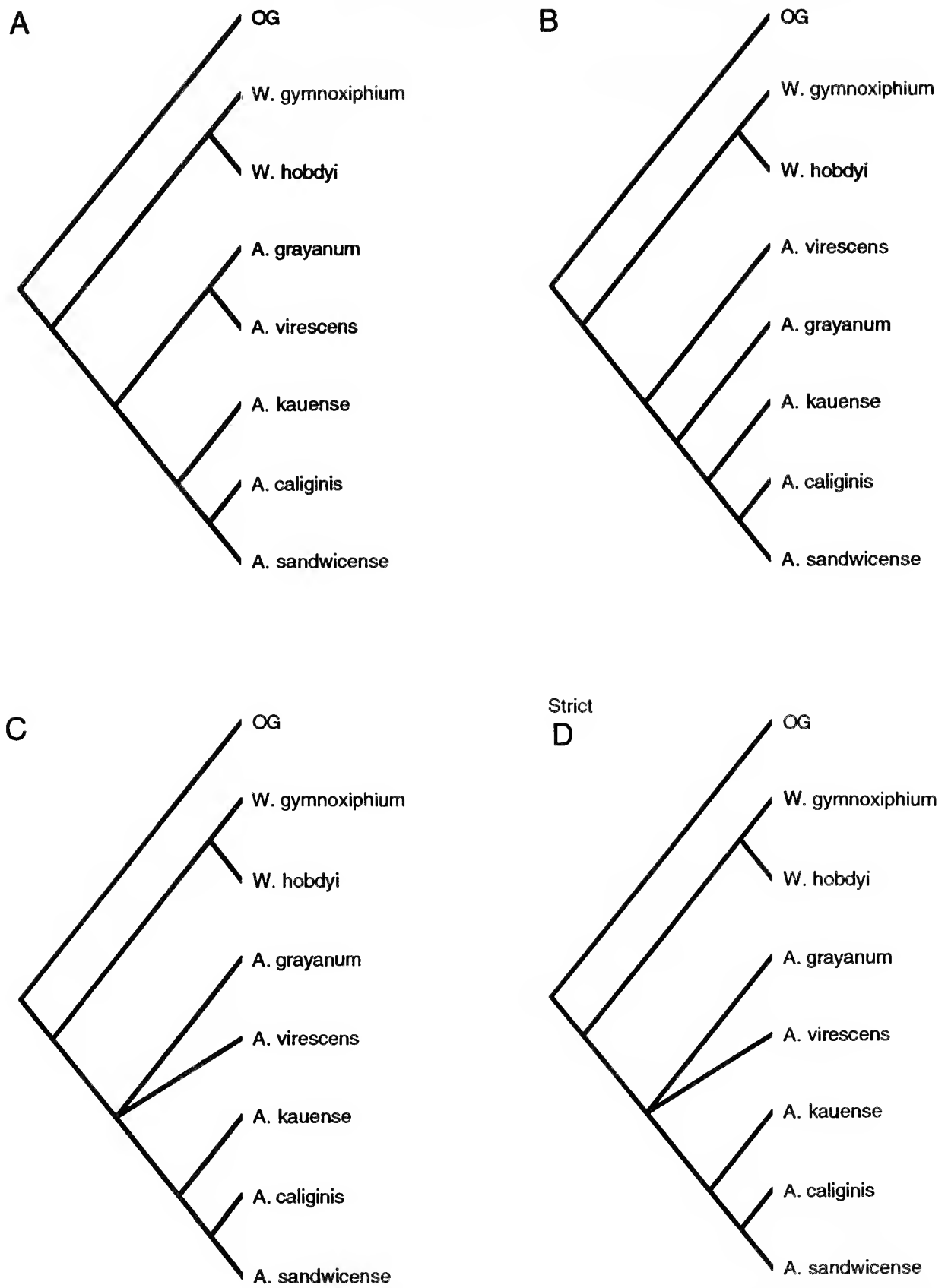


FIGURE 10.6. Three equally parsimonious cladograms and the strict consensus tree of *Argyroxiphium* and *Wilkesia*. (A to C) Three equally parsimonious topologies, with (C) as the least resolved and the same as the strict consensus tree. (D) Strict consensus tree. OG, outgroup.

sus tree for the ingroup taxa. All three arrangements involve a different position for *A. virescens*. Rerunning the analysis without *A. virescens* resulted in one tree with *A. grayanum* as the sister species to the rest of *Argyroxiphium*. The movement on the cladogram of *A. virescens* may indicate that it is a hybrid (Funk, 1985), which supports an earlier suggestion by Carr (1985). The third tree (Figure 10.6C), which places *A. virescens* in the least resolved position, is the same as the strict consensus tree (Figure 10.6D) and has been selected as the phylogeny to be used for the remainder of this discussion. Note, however, all three cladograms give the same result in the biogeographic analysis.

Two of the sections of *Dubautia* appear to be monophyletic, whereas the third section of *Dubautia* appears to be paraphyletic with respect to *Argyroxiphium* and *Wilkesia* and may possibly contain the common ancestor, or its descendants, of the latter two genera. *Wilkesia* is monophyletic as is *Argyroxiphium*, and both are more closely related to one another than either is to *Dubautia*. These results disagree with the molecular data (see Baldwin and Robichaux, this volume, Chapter 13) in two ways. First, the molecular data show three species of *Dubautia* to be the taxa most closely related to *Wilkesia*. However, the two species of *Wilkesia* are more closely related to one another than either is to any of the three *Dubautia* species. The species of *Dubautia* were not analyzed individually, and in the morphological analysis, this genus was indicated as paraphyletic, so it is possible that some of the species are more closely related to the *Wilkesia* clade than they are to *Dubautia*. The three species of *Dubautia* mentioned above are endemic to Kaua'i, as are both species of *Wilkesia*, so the resolution of the relationship of *Wilkesia* and these three *Dubautia* species does not alter the biogeographic conclusions.

The second difference between the morphological and the molecular analyses is that the morphological analysis shows *Wilkesia* and *Argyroxiphium* to be a monophyletic group whereas the DNA data suggest a closer relationship between *Dubautia* and *Wilkesia* than either genus has to *Argyroxiphium*. This discrepancy does not make a difference in the individual clades but does change the resolution at the base of the area cladogram. Only additional morphology and molecular data may help explain this discrepancy.

The cladogram, including outgroups, was converted into an area cladogram (Figure 10.7). The most-parsimonious arrangement indicates an ancestor to the group was located on Kaua'i with dispersal to Maui followed by two independent dispersal events to different volcanoes on Hawai'i, only one of which is associated with a speciation event. The

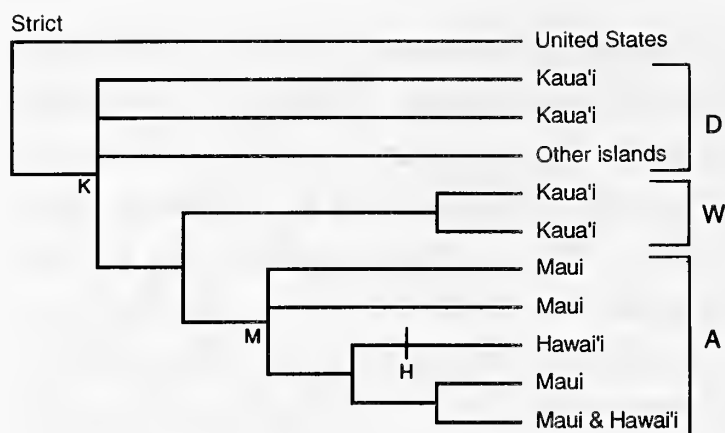


FIGURE 10.7. Area cladogram of the silversword alliance. The symbols are A, *Argyroxiphium*; D, *Dubautia*; and W, *Wilkesia*. K, Kaua'i; M, Maui; H, Hawai'i.

ambiguity at the base of the cladogram may be the result of several dispersal events of extinct taxa from now severely eroded islands to the northwest of Kaua'i. Clearly, of the current species, *Wilkesia* had an origin on Kaua'i and *Argyroxiphium* radiated out of Maui. The group as a whole is indicated to have its origin on Kaua'i. The geographic pattern shows colonization from older to younger islands. One possible contributing factor that may obscure overall biogeographic patterns is the absence of alpine habitat on the older islands. Most of the species of *Argyroxiphium* are confined to higher elevations (usually higher than 1,600 m) and thus cannot occur on any other islands besides Maui and Hawai'i. Although the extant *Argyroxiphium* clade appears to have originated on Maui, its ancestors could have originated on an older island that no longer has sufficient elevation to support the habitats needed for these species. Only one species, *A. grayanum*, grows below 1,600 m. It occurs in West Maui bogs at 1,200 m, and therefore it could grow on Kaua'i but has not been found there. Thus, it seems less likely that *A. grayanum* has dispersed from Kaua'i or other now-eroded islands, and more likely that the current species of *Argyroxiphium* had their origin on Maui.

Kokia

Kokia is a Hawaiian endemic genus in the Malvaceae with four species (see Figure 10.1D; Table 10.1), one extinct and the remaining three endangered. These red-flowered trees are characterized by having three large, foliaceous, involucral bracts (Appendix 10.9, TS 3), a unique zygomorphic corolla of twisted petals (TS 9), and a densely yellowish silky pubescence.

Ten transformation series were identified with 13 potentially useful characters (Appendixes 10.9 and 10.10). Of these characters, six were found to be informative, with seven available as potential synapomorphic

TABLE 10.6. Character Status for *Kokia*

| Transformation series ^a | Informative | Status | Characters |
|------------------------------------|-------------|----------|------------|
| 1 | Yes | Included | 01 |
| 2 | Yes | Included | 01 |
| 3 | Yes | Included | 012 |
| 4 | No | Ignored | 01 |
| 5 | Yes | Included | 01 |
| 6 | No | Ignored | 012 |
| 7 | No | Ignored | 012 |
| 8 | Yes | Included | 01 |
| 9 | No | Ignored | 01 |
| 10 | Yes | Included | 01 |
| 11 | No | Excluded | 01234 |

^aAll are unordered.

characters (Table 10.6). One of the species, *Kokia lanceolata*, has been extinct since the late 1800s or early 1900s; no specimens with fruits were ever collected. Four of the transformation series involve fruit characters (TS 5 to 8), and these were coded as missing for *K. lanceolata*.

In 1979, Fryxell suggested two genera as closely related to *Kokia*, *Thespesia*, and a sometimes recognized segregate, *Cephalohibiscus*. *Cephalohibiscus* is endemic to New Guinea and the Solomon Islands, and it has many autapomorphic characters that make it a poor choice for an outgroup for this analysis. *Thespesia* is pantropical (including the Pacific islands), has fewer autapomorphic characters, and therefore was selected as the outgroup.

The cladistic analysis resulted in three equally parsimonious trees. The multiple equally parsimonious trees were the result of the missing information for *Kokia lanceolata*. The trees differed in that *K. lanceolata* was variously placed as basal, as the sister group to *K. cookei*, or as the sister group to *K. kauaiensis* and *K. drynarioides*. In all three trees, *K. lanceolata* was spatially close to *K. cookei* on the cladogram, and it never violated the well-defined monophyletic group formed by *K. kauaiensis* and *K. drynarioides*. One of the three trees was selected as the phylogeny (Figure 10.8A) because it was identical to the single tree generated when the analysis was based only on the character distributions of the transformation series that were not missing any information. The tree length is 9, the CI is 0.889, and the RC is 0.741.

The species with the fewest number of apomorphic characters, *Kokia lanceolata* and *K. cookei*, occur on O‘ahu and Moloka‘i. *Kokia*

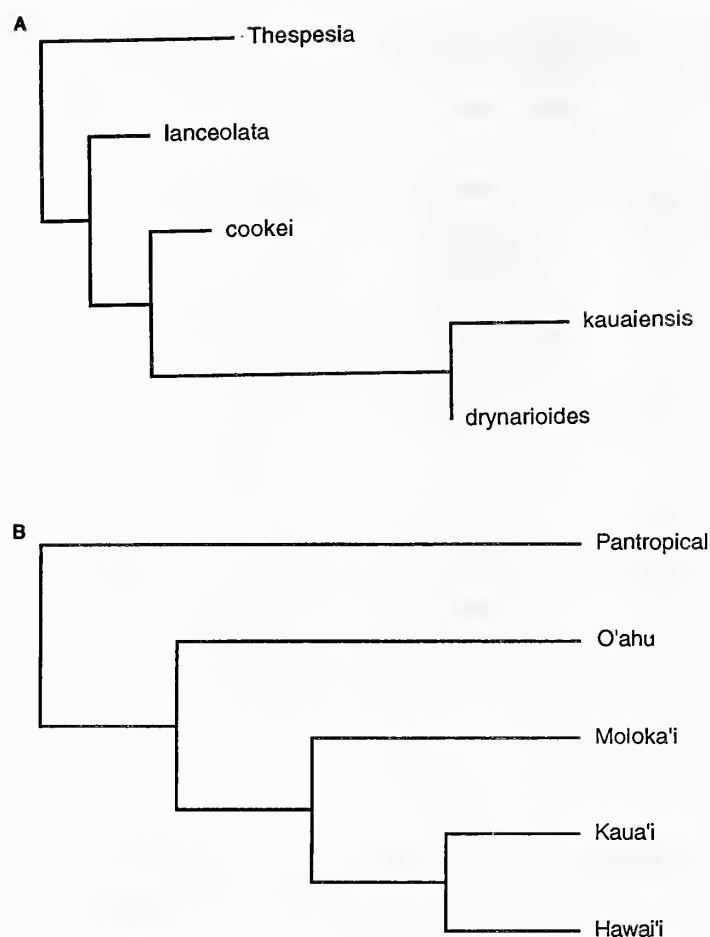


FIGURE 10.8. One of three equally parsimonious cladograms for *Kokia*; missing data for *K. lanceolata* accounted for the differences in topology among the three cladograms. (A) Phylogram; (B) area cladogram.

kauaiensis, the species with the largest number of apomorphic characters, is also the most recently derived and occurs on the oldest island, Kaua'i.

The area cladogram (Figure 10.8B) provides two interesting results. First is the problem that occurs when optimizing the distribution on an area cladogram when each taxon is on a different island. The result is simply a list of all the islands at the base of the area cladogram. However, when a ladderlike progression is assumed, dispersal from older to younger islands is apparent with one exception. Second, the pattern produced, oldest-to-youngest island (O'ahu to Moloka'i to Hawai'i), is interrupted by *Kokia kauaiensis* from Kaua'i, suggesting back-dispersal from Hawai'i. The pattern produced by the two other equally parsimonious cladograms does not conflict with these conclusions. The clade containing Hawai'i and Kaua'i is present in all three equally parsimonious cladograms (see discussion above), and it is the terminal group on all three trees. Therefore, all trees indicate that the species on Kaua'i is the result of a back-dispersal event. However, one additional hypothesis is possible. Because of the elimination of many dry forests before European exploration of the archipelago, dry forest species that are currently rare, such as *K. drynarioides*, may have had wider distributions in the past. If so, *K. drynarioides* could have occurred widely in the archipelago, pro-

viding a more common older-to-younger island dispersal pattern for this species and its sister species, *K. kauaiensis*.

Platydesma

Platydesma is an endemic Hawaiian genus of four species (see Figure 10.1E; Table 10.1), three of which are rare. The genus is believed to have arisen from an independent colonization event separate from all other Hawaiian Rutaceae (Stone, 1962; Stone et al., 1990). The genus is distinguished from other Rutaceae by its connate filaments (TS 13).

There are 14 transformation series with 17 potentially useful characters (Appendixes 10.11 and 10.12). Ten transformation series with 11 characters were found to be informative and therefore were available as potential synapomorphic characters (Table 10.7). Various groups have been suggested as ancestral to *Platydesma*. Stone (1962) proposed *Dutaillyea* (New Caledonia) or *Medicosma* (Australia) as possible relatives. More recently, T. Hartley (in Stone et al., 1990) disagreed with these hypotheses but offered no alternative suggestions as to the most closely related group. *Melicope* was selected as the outgroup for this study because it is a relatively large and widespread Pacific genus (Madagascar, Southeast Asia, Australia, Malaysia to New Zealand, and many Pacific islands) that appears to have many plesiomorphic characters.

TABLE 10.7. Character Status for *Platydesma*

| Transformation series ^a | Informative | Status | Characters |
|------------------------------------|-------------|----------|------------|
| 1 | Yes | Included | 01 |
| 2 | Yes | Included | 01 |
| 3 | Yes | Included | 01 |
| 4 | Yes | Included | 01 |
| 5 | No | Ignored | 012 |
| 6 | Yes | Included | 01 |
| 7 | Yes | Included | 01 |
| 8 | Yes | Included | 01 |
| 9 | Yes | Included | 01 |
| 10 | No | Ignored | 012 |
| 11 | Yes | Included | 012 |
| 12 | Yes | Included | 01 |
| 13 | No | Ignored | 01 |
| 14 | No | Ignored | 01 |
| 15 | Yes | Excluded | 01234 |

^aAll are unordered.

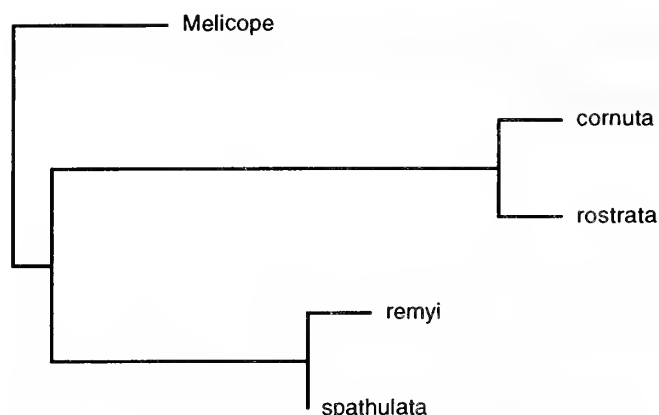


FIGURE 10.9. Single cladogram resulting from the analysis drawn as a phylogram for *Platydesma*.

The cladistic analysis resulted in one tree (Figure 10.9) with a length of 13, a CI of 1.0, and an RC of 1.0. The tree is divided into two symmetrical branches with one clade defined by four synapomorphic characters and the other by six. The *Platydesma cornuta*–*P. rostrata* clade (section *Cornutia*) has synapomorphic characters such as a palmoid leaf arrangement (TS 1) and sepals wider than long (TS 7), whereas the *P. remyi*–*P. spathulata* clade (section *Platydesma*) has subglobose fruits (TS 9) that are erect (TS 12).

The area cladogram (Figure 10.10) indicates that the two clades have quite different histories. Section *Cornutia* apparently originated on

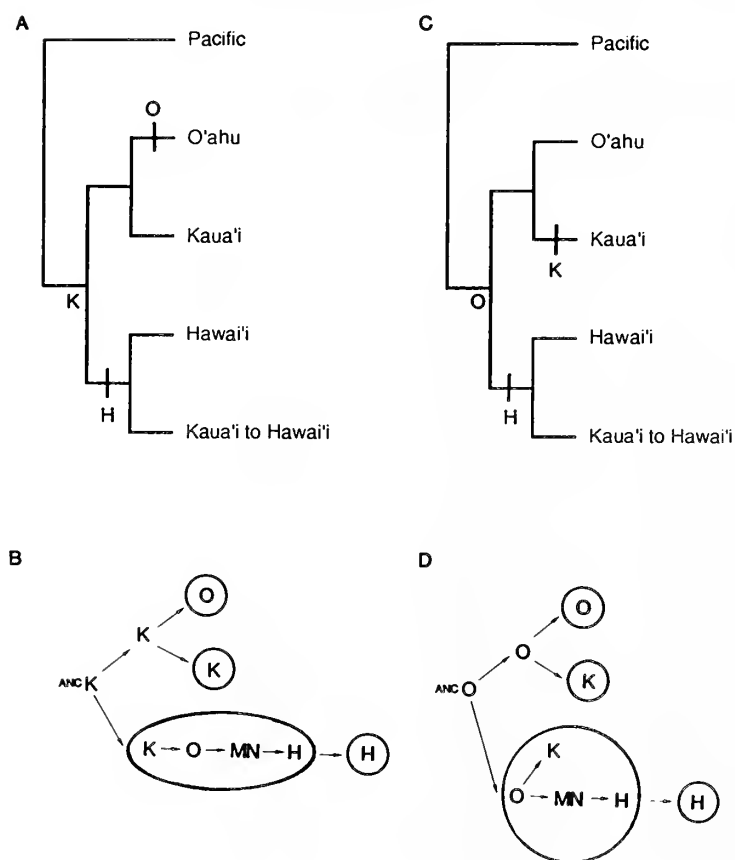


FIGURE 10.10. Two alternative area cladograms for *Platydesma*. (A) Area cladogram when the ancestor is assumed to have been on Kaua'i. (B) Schematic of inter-island colonization events for area cladogram in (A). (C) Area cladogram when the ancestor is assumed to have been on O'ahu. (D) Schematic of inter-island colonization events for area cladogram in (C). In (B) or (D), a circle around an island indicates the location of extant species, and an arrow indicates inter-island dispersal. K, Kaua'i; O, O'ahu; H, Hawai'i; ANC, ancestor; MN, Maui Nui complex.

Kaua'i and is restricted to two of the older islands, with *Platydesma cornuta* occurring on O'ahu and *P. rostrata* on Kaua'i. The other clade includes one species that has colonized throughout the archipelago and a second very closely related species endemic to Hawai'i. In fact, the Hawai'i species is most likely a minor segregate of the widespread *P. spathulata*. Because species are present on O'ahu and Kaua'i in both clades, either could be viewed as the ancestral location of the genus; both scenarios require an equal number of dispersal events. Figure 10.10A–B shows the ancestor on Kaua'i, which necessitates a dispersal event with speciation to O'ahu for *P. cornuta*. In this hypothesis, *P. spathulata* also arose on Kaua'i, followed by dispersal first to O'ahu, then to the Maui Nui complex, and finally to Hawai'i. Sometime while on Hawai'i, a population developed into *P. remyi*. The alternative hypothesis (Figure 10.10C and D) is that *Platydesma* originated on O'ahu and followed more or less the same pattern with one back-dispersal event with speciation to Kaua'i for *P. rostrata* and a separate back-dispersal event to Kaua'i from one of the younger islands for *P. spathulata*.

The different explanations of the history of *Platydesma spathulata* are possible because it has no autapomorphic characters. Because the second hypothesis requires a back-dispersal from a younger island to Kaua'i, we prefer the first hypothesis (Figure 10.10A and B). This hypothesis could be tested by a molecular or isozyme study and a numeric morphological analysis of the populations of *P. spathulata* to evaluate the relationships among the populations and, in particular, to determine whether the Hawai'i populations are more closely related to those on Kaua'i and Maui or just those on Maui. Finally, the area cladogram is consistent with the hypothesis that one or both of the clades originated on an older, now-eroded island and dispersed to Kaua'i to proceed across the chain to ever younger islands. Although both clades are quite distinctive, the species with the largest number of apomorphic characters are found on Kaua'i and O'ahu.

Geranium Section *Neurophyllodes*

The endemic Hawaiian species of the genus *Geranium* (Geraniaceae) form a monophyletic group defined by several characters, including woody stems (see Figure 10.1F; Appendix 10.13, TS 11), coriaceous leaves grouped at the tips of branches (TS 12), and exclusively parallel veined leaves (TS 10). The clade is distinctive enough to have been recognized at the sectional or even generic level. There is some dispute

TABLE 10.8. Character Status for *Geranium*

| Transformation series ^a | Informative | Status | Characters |
|---------------------------------------|-------------|----------|------------|
| 1 | No | Ignored | 01 |
| 2 | No | Ignored | 012 |
| 3 | No | Ignored | 01 |
| 4 | Yes | Included | 01 |
| 5 | No | Ignored | 01 |
| 6 | Yes | Included | 012 |
| 7 | No | Ignored | 012 |
| 8 | Yes | Included | 01 |
| 9 | Yes | Included | 0123 |
| 10 | No | Ignored | 01 |
| 11 | No | Ignored | 01 |
| 12 | No | Ignored | 01 |
| 13 | Yes | Included | 012 |
| 14 | Yes | Included | 01 |
| 15 | Yes | Included | 01 |
| 16 | Yes | Included | 01 |
| 17 | Yes | Included | 01 |
| 18 | Yes | Included | 01 |
| 19 | Yes | Included | 012 |
| 20 | No | Ignored | 01 |
| 21 | Yes | Included | 012 |
| 22 | No | Ignored | 01 |
| 23 | No | Excluded | 01234 |
| 24 | Yes | Excluded | 0123 |

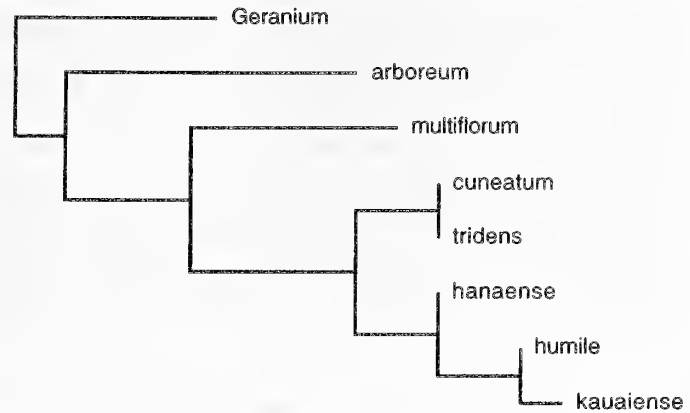
^aAll are unordered.

concerning the number of species that should be recognized (Carlquist and Bissing, 1976). After careful consideration, seven species were recognized for this analysis, which is one more than in the most recent treatment (Wagner et al., 1990) (see Table 10.1).

For the seven species of *Geranium*, there are 22 transformation series, 7 of which had 3 or more characters, for a total of 30 potentially useful characters (Appendixes 10.13 and 10.14). Of these, 18 were found to be informative (Table 10.8).

The outgroup for *Geranium* section *Neurophyllodes* is the remainder of the genus (ca. 300 species). The transformation series were divided into the following three categories: (1) Five of the series including leaves truncate at the apex (TS 16), densely strigulose pubescence on the leaf undersurface (TS 17), extensive rooting at the nodes (TS 8), the presence

FIGURE 10.11. Single cladogram resulting from the analysis drawn as a phylogram for *Geranium* section *Neurophyllodes*.



of complex compound cymes (TS 21), and others (TS 1, 2, 3, 5, 6, 14, 19, and 20), are unique to only part of the Hawaiian species and thus were easily polarized; (2) a few transformation series with characters such as sepal shape (TS 4), stipule length (TS 7), and others (TS 9 and 15) were ambiguous in the outgroup and were coded either as unknown or polymorphic; and (3) the final two transformation series (TS 13 and 18) were characterized by having one character that is pervasive in all the infrageneric groups of *Geranium* and this character was considered to be plesiomorphic.

The cladistic analysis resulted in one tree (Figure 10.11). The length of the tree is 22, the CI is 0.909, and the RC is 0.808.

The area cladogram (Figure 10.12A) shows that all internal nodes of the cladogram are most parsimoniously interpreted as being located on East Maui with one dispersal event to Hawai'i and two independent back-dispersal events, one to West Maui and one to Kaua'i. It is equally parsimonious to alternatively hypothesize a back-dispersal event from East Maui to West Maui, associated with speciation, followed by a back-dispersal event from West Maui to Kaua'i. However, the shorter dispersal distance of colonization from East Maui to West Maui and then to Kaua'i seems more likely. Also, the West Maui species, *Geranium humile*, has no autapomorphic characters to prevent it from being the ancestor of the Kaua'i species, *G. kauaiense*; however, the reverse is not true. Given the location of the two basal species, one might hypothesize an origin for the group on East Maui, and indeed this has been suggested by Carlquist and Bissing (1976). Our analysis only suggests the clade that contains the seven extant species originated on East Maui, not necessarily that it was the site of the original colonization. The Hawaiian species of *Geranium* have many unique characters distinguishing them from the rest of the genus, suggesting that a relatively recent arrival would be unlikely. It is possible that an island older than East Maui with subalpine habitat

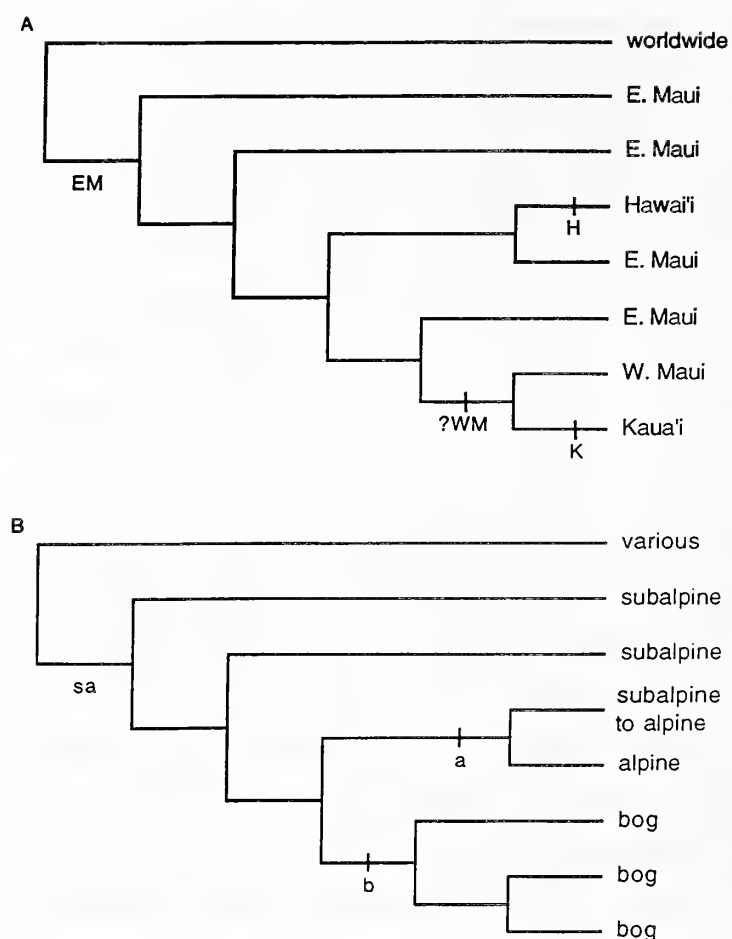


FIGURE 10.12. Cladograms with area and habitat traced onto them for *Geranium* section *Neurophyllodes*. (A) Area cladogram; (B) habitat hypothesis. EM, East Maui; H, Hawai'i; WM, West Maui; K, Kaua'i; sa, subalpine; a, alpine; and b, bog.

once harbored now-extinct species of *Geranium* that dispersed to the subalpine areas of East Maui.

Geranium arboreum is the species with the largest number of autapomorphic characters because it is the only bird-pollinated species among the Hawaiian geraniums (Wagner et al., 1990). It is also the basal branch on the cladogram. As in other lineages such as *Remya* and *Hesperomannia*, the basal position of this species indicates early divergence within the clade and should not be taken to mean that it contains the plesiomorphic characters of the clade.

Each of the four East Maui species occurs at or in a somewhat different elevation or habitat. For instance, *Geranium arboreum* and *G. multiflorum* both grow at the same elevation on Haleakala; however, the former is bird-pollinated and grows in gulches but is perhaps restricted there because of severe habitat perturbation, whereas the latter is insect-pollinated and grows in alpine shrubland.

The habitats of the species correlate well with the cladogram in that the basal two species grow in subalpine areas, the two species on the next branch grow in subalpine to alpine areas, and the terminal clade grows in midelevation bogs (Figure 10.12B). One explanation based on this cladogram would be that the ancestor of this clade was a subalpine species

when it arrived on East Maui, followed by evolution in two different directions. In one clade, there was a gradual shift into alpine habitats followed by dispersal to Hawai'i, whereas the other clade moved into midelevation bogs followed by back-dispersal to West Maui and Kaua'i. All available subalpine and alpine areas and bogs of substantial size and constancy in the archipelago have species of *Geranium* growing in them.

DISCUSSION

The purpose of this study was to determine if the seven selected lineages shared any patterns that might give some insights into the biogeography and speciation of Hawaiian plants. Comparing the results of the analyses elucidated several patterns.

Many of the lineages exhibit an older-to-younger island dispersal pattern where the analysis shows that the basal taxa occur on the older islands. *Remya* has a Kaua'i-to-West Maui dispersal pattern, whereas *Hesperomannia* shows a Kaua'i-to-O'ahu pattern, followed by further colonization without speciation. *Platydesma* is divided into two clades, each of which may have originated on Kaua'i. One dispersed to O'ahu and the other throughout the younger islands. These two clades may represent independent colonizations of Kaua'i from an older, now severely eroded island. The *Wilkesia-Argyroxiphium* clade has the basal branches on Kaua'i followed by dispersal and then speciation on Maui with two subsequent dispersal events to Hawai'i. *Hibiscadelphus* shows a dispersal from Kaua'i to the Maui Nui complex followed by another to Hawai'i, with a radiation on several different volcanoes on Hawai'i. All these patterns are consistent with an older-to-younger island dispersal.

A second pattern can be seen in *Kokia*, where the pattern is consistent with an older-to-younger island pattern, Kaua'i to Moloka'i to Hawai'i, but there is a back-dispersal event to Kaua'i accompanied by speciation. However, if widespread elimination of populations of *K. drynarioides* occurred, then *Kokia*, too, follows an older-to-younger island pattern.

A final pattern involves a clear younger-to-older island colonization. The *Geranium* clade originated on East Maui with dispersal in two directions, one to Hawai'i and the other probably first to West Maui and then to Kaua'i. However, although this clade clearly originated on Maui, its ancestors may have been present on older islands.

Although the predominant pattern in the groups we studied exhibits the basal taxon on the oldest high island, using this species as the outgroup for the rest of the species would be misleading and could cause serious problems with an analysis. In several instances, the species on Kaua'i, even when basal, do not necessarily have large numbers of plesiomorphic characters. In several groups, the species with the greatest number of derived characters occur on the older islands (e.g., *Remya*). Likewise, the basal branch of *Hesperomannia* is on Kaua'i and has the largest number of apomorphic characters, whereas the most recent clade is poorly defined and occurs on several younger islands. Finally, in *Platydesma*, the clade confined to the older islands has the most apomorphic characters.

The opposite condition also occurs, in which terminal taxa on younger islands have the most apomorphic characters. The clades comprising *Wilkesia* and *Argyroxiphium* are both well supported, one on Kaua'i and the other on Maui and Hawai'i. The species with the most autapomorphic characters is *A. caliginis* on West Maui. Similarly, in *Hibiscadelphus*, the species with the most autapomorphic characters occurs on Mauna Loa, Hawai'i; in fact, the entire clade with the species from the younger islands is well supported and quite distinct. In *Kokia*, the terminal clade is the best-supported group, and it has one species on Hawai'i and one on Kaua'i (possible back-dispersal), whereas in *Geranium*, the basal species is on a younger island and has many apomorphic characters. There is also little correlation between the geographic distribution of a species and the number of apomorphic characters that it possesses. For instance, *Hesperomannia arborescens* is widespread on several islands and has several apomorphic characters, whereas *Platydesma spathulata* occurs nearly throughout the main islands and has few apomorphic characters.

Area cladograms can be used to study patterns of speciation and radiation. One can determine the number of inter-island speciation events that are necessary to explain the various patterns. For instance, *Hibiscadelphus* and *Kokia* require three allopatric speciation events, the *Wilkesia-Argyroxiphium* and *Geranium* clades two events, and *Remya* and *Platydesma* one event. When more than one species of a lineage is on an island, the area cladogram can be used to separate independent colonization from adaptive radiation. The latter is indicated in *Geranium* on East Maui where the species shift from subalpine habitat to bogs and alpine sites, on Hawai'i where three species of *Hibiscadelphus* have developed, and in *Wilkesia* on Kaua'i and *Argyroxiphium* on Maui.

However, independent colonization can explain the Hawai'i Island species of *Argyroxiphium* and the O'ahu species of *Platydesma*.

Cladograms of extant species do not preclude an older origin for a lineage, they simply give the evolutionary history of the extant clade. Several groups (e.g., *Geranium*, the silverswords, and *Platydesma*) give some indication that they might have been present on older, now-submerged islands. Certainly, there are remnants of large higher islands in the leeward chain that may well have had appropriate habitat.

CONCLUSIONS

The results of these analyses show that phylogenetic analyses can be very informative concerning the relationships among the plant lineages of the Hawaiian Islands. The cladograms indicate a strong tendency for colonization within these endemic lineages to be from older to younger islands, often resulting in speciation. However, incidents of back-dispersal as well as the origin of clades on younger islands can also be identified. The analyses in this chapter also show that a biogeographic assessment can provide insights into the patterns of speciation. They similarly indicate intra-island radiations and independent inter-island dispersal events. Clearly, such studies contribute to the overall knowledge of the history of the biological diversity of the Hawaiian Islands.

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APPENDIX 10.1. Transformation Series for *Hibiscadelphus*

1. Calyx length: 0 = <2.5 cm; 1 = 2.7–4.2 cm; 2 = >4.2 cm.
2. Calyx: 0 = persistent; 1 = deciduous.
3. Capsules: 0 = chartaceous; 1 = woody.
4. Capsule apex: 0 = apiculate; 1 = invaginate; 2 = beaked.
5. Capsule length: 0 = <1.7 cm; 1 = 2.2–3.0 cm; 2 = 3.5 cm; 3 = 4–5 cm.
6. Endocarp segments: 0 = 5; 1 = 1.0.

7. Involucral bract shape: 0 = narrowly linear–narrowly triangular; 1 = linear–spathulate; 2 = tooth-like; 3 = filiform.
8. Leaf shape: 0 = unlobed; 1 = 3–5 angled.
9. Leaf base: 0 = sinus open; 1 = sinus closed; 2 = overlapping.
10. Petiole length: 0 = <1 cm; 1 = 1–5 cm; 2 = 4–10 cm; 3 = 10–25 cm.
11. Involucral bract base: 0 = not connate; 1 = connate slightly; 2 = connate over 1/3 length.
12. Involucral bract: 0 = 0.5–2.0 mm; 1 = 9–10 mm; 2 = 11–18 mm; 3 = 18–35 mm.
13. Corolla type: 0 = actinomorphic; 1 = two lower petals shorter.
14. Corolla shape: 0 = campanulate; 1 = narrowly convolute.
15. Distribution: 0 = worldwide; 1 = Kaua‘i; 2 = Lana‘i; 3 = East Maui; 4 = Hawai‘i (not used in analysis).
16. Distribution: 0 = worldwide; 1 = Kaua‘i; 2 = Maui Nui; 3 = Hawai‘i (not used in analysis).

APPENDIX 10.2. Data Matrix of Characters of *Hibiscadelphus*

The transformation series and characters are defined in Appendix 10.1. TS 15 and 16 are distributions and were not used in the analysis. A question mark indicates an unknown character.

| Taxon | Transformation series | | | | | | | | | | | | | | | |
|---|-----------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
| <i>Hibiscus</i> | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Hibiscadelphus</i> <i>wilderianus</i> | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 2 | 1 | 2 | 1 | 1 | 3 | 2 |
| <i>Hibiscadelphus</i> <i>hualalaiensis</i> | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 4 | 3 |
| <i>Hibiscadelphus</i> <i>giffardianus</i> | 1 | 1 | 1 | 1 | 3 | 1 | 3 | 1 | 2 | 3 | 1 | 3 | 1 | 1 | 4 | 3 |
| <i>Hibiscadelphus</i> <i>distans</i> | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 2 | 1 | 1 | 1 | 1 |
| <i>Hibiscadelphus</i> <i>crucibracteatus</i> | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 3 | 1 | 1 | 2 | 2 |
| <i>Hibiscadelphus</i> <i>bombycinus</i> | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 4 | 3 |
| <i>Hibiscadelphus</i> sp. nov. | 2 | 0 | ? | ? | ? | ? | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |

APPENDIX 10.3. Transformation Series for *Remya*

1. Habit: 0 = sprawling shrub; 1 = vine in canopy.
2. Pubescence: 0 = white tomentose; 1 = glabrous.

- 3. Leaf base: 0 = attenuate; 1 = cuneate.
- 4. Leaves: 0 = chartaceous; 1 = thin.
- 5. Leaf margin: 0 = serrate; 1 = doubly irregularly serrate.
- 6. Inflorescence: 0 = open panicle; 1 = compact panicle.
- 7. Peduncle: 0 = thin; 1 = stout.
- 8. Peduncle length: 0 = 0–5 mm; 1 = 8–15 mm.
- 9. Peduncle color: 0 = green; 1 = purple.
- 10. Involucre height/width: 0 = 1; 1 = 2; 2 = 0.5.
- 11. Involucral bract apex: 0 = attenuate; 1 = obtuse.
- 12. Ray number: 0 = 12–14; 1 = 16–20.
- 13. Ray length: 0 = small; 1 = vestigial.
- 14. Outer disk florets: 0 = staminate; 1 = few pistillate; 2 = neutral.
- 15. Inner disk florets: 0 = hermaphroditic; 1 = staminate.
- 16. Disk floret shape: 0 = tubular; 1 = upper part hemispheric.
- 17. Ray pappus: 0 = many barbellate bristles; 1 = reduced, flat, and few.
- 18. Disk pappus: 0 = 2–3 long others short; 1 = all short and subequal; 2 = absent.
- 19. Distribution: 0 = Old World; 1 = Kaua‘i; 2 = West Maui (not used in analysis).

APPENDIX 10.4. Data Matrix of Characters of *Remya*

The transformation series and characters are defined in Appendix 10.3. TS 19 is the distribution and was not used in analysis. Polymorphic characters are a = 0/1.

| Taxon | Transformation series | | | | | | | | | | | | | | | | | | |
|-----------------------|-----------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
| <i>Olearia</i> | 0 | a | 0 | 0 | 0 | a | a | a | 0 | a | a | a | 0 | 0 | 0 | 0 | 0 | 0 | a |
| <i>R. kauaiensis</i> | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| <i>R. mauiensis</i> | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| <i>R. montgomeryi</i> | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 2 | 1 |

APPENDIX 10.5. Transformation Series for *Hesperomannia*

- 1. Young stems and leaves: 0 = tomentose; 1 = glabrous.
- 2. Blade length/width: 0 = 2–4× as long as wide; 1 = <2; 2 = >4.
- 3. Head height: 0 = <5 cm; 1 = >5 cm.
- 4. Head orientation: 0 = ascending; 1 = pendulous.
- 5. Peduncles: 0 = short; 1 = long.
- 6. Peduncles: 0 = thick; 1 = thin.
- 7. Peduncles: 0 = pubescent; 1 = glabrous.
- 8. Involucre: 0 = <3.5 cm; 1 = >4 cm.

- 9. Inner involucral bracts: 0 = <2.3 cm; 1 = 2.3–2.8 cm; 2 = >3.7 cm.
- 10. Pappus color: 0 = purple; 1 = pale.
- 11. Anatomy of involucre: 0 = bundles occur only in interstices between the strands of fibers; 1 = bundles form a continuous band (see Carlquist, 1957b).
- 12. Anthers and stigma: 0 = erect; 1 = flopping.
- 13. Leaf margins: 0 = entire; 1 = serrate.
- 14. Pappus apex: 0 = tapering gradually; 1 = spatulate.
- 15. Flower color: 0 = white; 1 = yellow to yellow-brown.
- 16. Sclerified cells in corolla: 0 = absent; 1 = present (see Carlquist, 1957a).
- 17. Pappus: 0 = plumose or glabrous; 1 = scabrous.
- 18. Petiole: 0 = short; 1 = long and slender.
- 19. Distribution: 0 = South America; 1 = Kaua‘i; 2 = O‘ahu; 3 = Moloka‘i; 4 = Lana‘i; 5 = West Maui (not used in analysis).

APPENDIX 10.6. Data Matrix of Characters of *Hesperomannia*

The transformation series and characters are defined in Appendix 10.5. TS 19 is the distribution and was not used in the analysis. A question mark indicates an unknown character. Polymorphic characters are a = 0/1, b = 2/3/4, c = 2/5.

| Taxon | Transformation series | | | | | | | | | | | | | | | | | | |
|-----------------------|-----------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
| <i>Stifftia</i> | 0 | 0 | a | 0 | a | a | a | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>H. arborescens</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | b |
| <i>H. arbuscula</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | c |
| <i>H. lydgatei</i> | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 |

APPENDIX 10.7. Transformation Series for *Argyroxiphium* and *Wilkesia*

- 1. Color of pubescence: 0 = green; 1 = gray.
- 2. Leaf shape: 0 = elliptic to linear; 1 = narrowly swordshaped; 2 = elliptically swordshaped.
- 3. Leaf cross section: 0 = round; 1 = triangular.
- 4. Leaf base: 0 = free; 1 = partially connate; 2 = fused and whorled.
- 5. Rachis: 0 = thin; 1 = proximally fistulose; 2 = fistulose.
- 6. Veins: 0 = prominent; 1 = obscure.
- 7. Ray flowers: 0 = absent; 1 = present.
- 8. Disk flowers: 0 = glandular; 1 = glands absent.
- 9. Leaf bases: 0 = lost; 1 = retained.
- 10. Ventral pappus length: 0 = same as dorsal; 1 = shorter; 2 = greatly reduced; 3 = absent.

- 11. Rosettes on elevated woody stems: 0 = no; 1 = yes.
- 12. Number of heads per inflorescence: 0 = <50; 1 = usually >50 but <350; 2 = usually >350.
- 13. Disk flower color: 0 = white or yellow (sometimes tinged with purple); 1 = purple.
- 14. Inner involucral bract: 0 = enfolding; 1 = not enfolding.
- 15. Corolla tubes: 0 = glabrous; 1 = setulose.
- 16. Pectic channels in leaf: 0 = no; 1 = yes.
- 17. Vascular bundles: 0 = many; 1 = few.
- 18. Pappus: 0 = scales; 1 = aristae.
- 19. Distribution: 0 = United States ; 1 = Kaua‘i; 2 = O‘ahu; 3 = Maui; 4 = Hawai‘i (not used in anaysis).

APPENDIX 10.8. Data Matrix of Characters of *Argyroxiphium* and *Wilkesia*

The transformation series and characters are defined in Appendix 10.7. TS 19 is the distribution and was not used in the analysis. Polymorphic characters are a = 0/1, b = 2/3/4, c = 3/4.

| Taxon | Transformation series | | | | | | | | | | | | | | | | | | |
|---------------------------|-----------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
| Tarweeds | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Dubautia</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| <i>Venoso-reticulatae</i> | | | | | | | | | | | | | | | | | | | |
| <i>D. Dubautia</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 1 |
| <i>D. Railliardia</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | b |
| <i>W. gymnoxiphium</i> | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>W. hobdyi</i> | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>A. grayanum</i> | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | a | 3 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 3 |
| <i>A. virescens</i> | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 3 |
| <i>A. kauense</i> | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 4 |
| <i>A. caliginis</i> | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 3 |
| <i>A. sandwicense</i> | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | c |

APPENDIX 10.9. Transformation Series for *Kokia*

- 1. Leaf blade lower surface pubescense location: 0 = vein axils; 1 = near base.
- 2. Leaf base shape: 0 = cordate; 1 = subtruncate.
- 3. Involucral bract shape: 0 = longer than wide; 1 = almost as wide as long; 1 = as wide as or wider than long.

- 4. Staminal column length: 0 = >1 cm; 1 = <7.
- 5. Capsule shape: 0 = globose; 1 = ovoid.
- 6. Capsule apex: 0 = invaginate or truncate; 1 = apiculate; 2 = acuminate.
- 7. Trichome length on seed: 0 = <1 mm; 1 = 3 mm; 2 = 1 mm.
- 8. Seed length: 0 = 8–15 mm; 1 = 2 mm.
- 9. Corolla shape: 0 = campanulate; 1 = twisted.
- 10. Leaf base fusion: 0 = open; 1 = closed.
- 11. Distribution: 0 = pantropical; 1 = Kaua‘i; 2 = O‘ahu; 3 = Moloka‘i; 4 = Hawai‘i (not used in analysis).

APPENDIX 10.10. Data Matrix of Characters of *Kokia*

The transformation series and characters are defined in Appendix 10.9. TS 11 is the distribution and was not used in the analysis. A question mark indicates an unknown character. Polymorphic characters are a = 0/1.

| Taxon | Transformation series | | | | | | | | | | |
|------------------------|-----------------------|---|---|---|---|---|---|---|---|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| <i>Thespesia</i> | 0 | a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>K. lanceolata</i> | 0 | 1 | 0 | 0 | ? | ? | ? | ? | 1 | 0 | 2 |
| <i>K. kauaiensis</i> | 1 | 0 | 2 | 0 | 1 | 2 | 2 | 0 | 1 | 1 | 1 |
| <i>K. drynarioides</i> | 1 | 0 | 2 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 4 |
| <i>K. cookei</i> | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 3 |

APPENDIX 10.11. Transformation Series for *Platydesma*

- 1. Habit: 0 = shrub or shrubby tree; 1 = palmoid.
- 2. Leaf thickness: 0 = coriaceous; 1 = soft.
- 3. Leaf color on lower surface: 0 = green; 1 = pale.
- 4. Pubescence on new growth and inflorescence: 0 = hirtellous; 1 = glabrous or yellow-brown.
- 5. Flower number: 0 = 3–9; 1 = 9–15; 2 = 1–3.
- 6. Pedicels: 0 = long; 1 = short.
- 7. Sepal size: 0 = longer than wide; 1 = wider than long.
- 8. Petal size: 0 = short; 1 = long.
- 9. Fruit: 0 = cruciate; 1 = subglobose.
- 10. Carpel apex: 0 = not beaked; 1 = short-beaked; 2 = long-beaked.
- 11. Seeds per carpel: 0 = 2; 1 = 5–8; 2 = 8.
- 12. Presentation of fruits: 0 = pendulous; 1 = erect.
- 13. Filaments: 0 = distinct; 1 = connate.
- 14. Carpels: 0 = distinct; 1 = connate.
- 15. Distribution: 0 = Pacific; 1 = Kaua‘i; 2 = O‘ahu; 3 = Maui; 4 = Hawai‘i (not used in analysis).

APPENDIX 10.12. Data Matrix of Characters of *Platydesma*

The transformation series and characters are defined in Appendix 10.11. TS 15 is the distribution and was not used in the analysis. A question mark indicates an unknown character. Polymorphic characters are a = 0/1, b = 1/2/3/4.

| Taxon | Transformation series | | | | | | | | | | | | | | |
|----------------------|-----------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| <i>Melicope</i> | 0 | 0 | a | ? | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>P. cornuta</i> | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 2 |
| <i>P. remyi</i> | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 4 |
| <i>P. rostrata</i> | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 1 |
| <i>P. spathulata</i> | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | b |

APPENDIX 10.13. Transformation Series for *Geranium*

1. Corolla shape: 0 = actinomorphic; 1 = zygomorphic.
2. Corolla color: 0 = pink-purple; 1 = white; 2 = magenta.
3. Sepal length: 0 = 5–10 mm; 1 = 12–16 mm.
4. Sepal shape: 0 = elliptic to oblanceolate; 1 = lanceolate.
5. Styler column length: 0 = 5–10 mm; 1 = 10–15 mm.
6. Leaf margin: 0 = palmately divided; 1 = serrate near apex; 2 = toothed at apex.
7. Stipule length: 0 = 5–10 mm; 1 = 3–5 mm; 2 = 12–14 mm.
8. Stem rooting: 0 = no; 1 = yes.
9. Plant height: 0 = decumbent; 1 = 3–10 dm; 2 = 10–20 dm; 3 = 20–40 dm.
10. Pinnate leaf venation: 0 = present; 1 = absent.
11. Stems woody: 0 = no; 1 = yes.
12. Leaf position: 0 = along stem; 1 = at apex of stem only.
13. Flower number: 0 = few; 1 = some; 2 = many.
14. Sepal apex: 0 = awn; 1 = mucronate.
15. Carpel pubescence: 0 = dense; 1 = sparse.
16. Leaf apex: 0 = acute; 1 = truncate.
17. Leaf pubescence on lower surface: 0 = moderately hirsute; 1 = densely silky strigulose.
18. Glandular trichomes: 0 = present; 1 = absent.
19. Flower position: 0 = born on axillary branches of standard length; 1 = born on very short axillary branches; 2 = born in more or less terminal cymes.
20. Location of flowers: 0 = spread out along branch; 1 = near tips of branches.
21. Cyme structure: 0 = simple; 1 = moderately branched; 2 = complex compound cymes.
22. Cymes: 0 = leafy; 1 = leafless.
23. Distribution: 0 = worldwide; 1 = Hawai‘i; 2 = East Maui; 3 = West Maui; 4 = Kaua‘i (not used in analysis).
24. Habitat: 0 = various; 1 = subalpine; 2 = alpine; 3 = midelevation bogs (not used in analysis).

APPENDIX 10.14. Data Matrix of Characters of *Geranium*

The transformation series and characters are defined in Appendix 10.13. TS 23 and 24 are distribution and habitat and were not used in the analysis. A question mark indicates an unknown character. Polymorphic characters are a = 0/1.

| Taxon | Transformation series | | | | | | | | | | | | | | | | | | | | | | | |
|-----------------------|-----------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |
| <i>Geranium</i> | 0 | 0 | 0 | a | 0 | 0 | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>G. arboreum</i> | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 3 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 |
| <i>G. cuneatum</i> | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 2 |
| <i>G. hanaense</i> | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 3 |
| <i>G. humile</i> | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 3 | 3 |
| <i>G. kauaiense</i> | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 4 | 3 |
| <i>G. multiflorum</i> | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 |
| <i>G. tridens</i> | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 2 |

11

Phylogeny, Adaptive Radiation, and Biogeography of Hawaiian *Tetramolopium* (Asteraceae, Astereae)

TIMOTHY K. LOWREY

Tetramolopium (Asteraceae, Astereae) is a wholly insular genus of small shrubby perennial plants. The genus has an unusual disjunct distribution, occurring in the Hawaiian Islands and New Guinea, with the recent discovery of a new species in the Cook Islands that is closely related to Hawaiian taxa (Lowrey, 1986; T. Lowrey, unpubl.). Eleven Hawaiian species are currently recognized (Table 11.1) (Lowrey, 1986) and approximately 25 species are recognized from New Guinea (Royen, 1983). Based on available taxonomic and geologic evidence, the genus likely evolved in New Guinea as a neo-endemic in the early Pleistocene and was subsequently dispersed to the Hawaiian Islands (Smith, 1977). The affinities of *Tetramolopium* clearly support this contention. The closest relatives of *Tetramolopium* are the genera *Eurybiopsis*, *Vittadinia*, and *Camptacra*, which are closely related, largely Australian taxa with a few species in New Zealand and New Guinea (Burbidge, 1982).

Fosberg (1948) suggested that the Hawaiian assemblage of *Tetramolopium* probably developed from a single colonization event by an Indo-Pacific progenitor that subsequently speciated forming a monophyletic group. Extensive biosystematic studies (Lowrey, 1981, 1986; Lowrey and Crawford, 1985) provide strong support for the monophyletic origin of and genetic cohesion in the Hawaiian taxa, based on cytogenetic, hybridization, and isozyme investigations. These Hawaiian taxa are diploid with $x = 9$. Interfertility among the species has been documented, with F_1 , F_2 , and F_3 hybrid progeny having been produced

TABLE 11.1. Growth Habit, Habitat, Elevational Range, and Island Distribution of Hawaiian *Tetramolopium* Arranged by Sectional Classification

| Taxon | Habit | Habitat | Elevational range (m) | Distribution |
|--|-------------|--------------------------------------|--------------------------|---|
| Section <i>Alpinum</i> | | | | |
| <i>T. humile</i> (A. Gray) Hillebr. | | | | |
| subsp. <i>haleakalae</i> Lowrey | Dwarf shrub | Subalpine woodland, alpine desert | 1,900–3,300 | East Maui |
| subsp. <i>humile</i> var. <i>humile</i> | Dwarf shrub | Subalpine woodland, alpine desert | 1,900–3,300 | East Maui, Hawai'i |
| subsp. <i>humile</i> var. <i>sublaeve</i> Sherff | Dwarf shrub | Subalpine woodland, alpine desert | 1,900–3,300 | Hawai'i (between Mauna Loa and Mauna Kea) |
| Section <i>Sandwicense</i> | | | | |
| <i>T. arenarium</i> (A. Gray) Hillebr. | | | | |
| subsp. <i>arenarium</i> var. <i>arenarium</i> | Shrub | Dry forest | 800–1,500 | East Maui, Hawai'i |
| subsp. <i>arenarium</i> var. <i>confertum</i> Sherff | Shrub | Dry forest | 800–1,500 | Hawai'i |
| subsp. <i>laxum</i> Lowrey | Shrub | Dry forest | 800–1,500 | East Maui |
| <i>T. consanguineum</i> (A. Gray) Hillebr. | | | | |
| subsp. <i>consanguineum</i> | Shrub | Dry forest | 200–1,600 | Hawai'i |
| subsp. <i>leptophyllum</i> (Sherff) Lowrey var. <i>kauense</i> Lowrey | Shrub | Dry forest | 200–1,600 | Hawai'i |

| | | | | |
|--|-----------------|--|-------------|------------------------------------|
| subsp. <i>leptophyllum</i> (Sherff) Lowrey var. <i>leptophyllum</i> | Shrub | Dry forest | 200–1,600 | Hawai‘i |
| <i>T. conyzoides</i> (A. Gray) Hillebr. | Shrub | Dry forest, coastal shrubland | 100–2,000 | Moloka‘i, Lana‘i, Maui, Hawai‘i |
| <i>T. lepidotum</i> (Less.) Sherff | | | | |
| subsp. <i>arbusculum</i> (A. Gray) Lowrey | Shrub | Grassy flats, cliff faces, mesic forest | 600–900 | Maui |
| subsp. <i>lepidotum</i> | Shrub | Grassy flats, cliff faces, dry forest | 600–900 | Lana‘i, O‘ahu |
| Section <i>Tetramolopium</i> | | | | |
| <i>T. capillare</i> (Gaud.) St. John | Sprawling shrub | Dry forest and shrubland | 1,000–3,000 | West Maui |
| <i>T. filiforme</i> Sherff | | | | |
| var. <i>filiforme</i> | Dwarf shrub | Dry ridges | 580–900 | O‘ahu |
| var. <i>polyphyllum</i> (Sherff) Lowrey | Dwarf shrub | Dry ridges | 580–900 | O‘ahu |
| <i>T. renyi</i> (A. Gray) Hillebr. | Decumbent shrub | Dry ridges | 150–300 | Lana‘i |
| <i>T. rockii</i> Sherff | | | | |
| var. <i>calcisabulorum</i> (St. John) Lowrey | Prostrate shrub | Coastal shrubland (lithified dunes) | 10–200 | Moloka‘i |
| var. <i>rockii</i> | Prostrate shrub | Coastal shrubland (lithified dunes) | 10–200 | Moloka‘i |
| <i>T. sylvae</i> Lowrey | Prostrate shrub | Cliffs | 20–1,000 | Moloka‘i, West Maui |
| <i>T. tenerimum</i> (Less.) Nees | Decumbent shrub | Unknown | 1,000 (?) | O‘ahu? |



FIGURE 11.1. Hawaiian *Tetramolopium* species representative of the three recognized taxonomic sections. Plants were raised from seed in the greenhouse. Left to right: *T. lepidotum*, *T. rockii*, and *T. humile*. Bar = 4.6 cm.

from all possible combinations (Lowrey, 1986). High fertility of the hybrids is supported by pollen stainabilities generally greater than 80%, normal bivalent chromosome pairing and disjunction, and production of viable cypsels (Lowrey, 1986). Although there is no documented instance of natural interspecific hybridization in Hawaiian *Tetramolopium*, there is one species, *T. filiforme* Sherff, that may represent an ancient intersectional hybridization event (Lowrey, 1986). Among the species of *Tetramolopium*, genetic identities derived from isozyme analysis are consistent with those obtained from comparisons of conspecific populations of mainland species (Lowrey and Crawford, 1985).

Despite this degree of genetic similarity, the Hawaiian species are ecologically and morphologically distinct. In the Hawaiian Islands, *Tetramolopium* species occupy a diversity of submesic to xeric habitats ranging from sea level to the alpine zone at 3,000 m, on five main Hawaiian Islands (O'ahu, Moloka'i, Maui, Lana'i, and Hawai'i). The diversity in elevational and ecological distribution represented by the species is correlated with a rather diverse array of life form, which includes prostrate coastal shrubs with succulent leaves, cespitose alpine shrublets, and forest shrubs up to 2 m in height (Figure 11.1). In contrast, the New Guinean taxa are largely cespitose alpine shrublets occurring exclusively in submesic or mesic habitats in the tropic-alpine zones above 2,000 m. The Hawaiian *Tetramolopium* species exhibit a diversity in

their sexual systems that is unknown in their New Guinea relatives. One group of five species is gynomonoeious (heads with female ray florets and bisexual disk florets), whereas the remaining six species are monoecious (heads with female ray florets and functionally staminate disk florets) (Lowrey, 1986). Several morphological characters are correlated with differences in sex expression, including capitulescence type, floret number per head, ligule length, head size, and floret color. Based on the diversity represented by the Hawaiian taxa, Lowrey (1986) subdivided the genus into three taxonomic sections, although previous workers have treated these as different genera.

Given the ecological and morphological diversity in Hawaiian *Tetramolopium* and the strong evidence for monophyly among the taxa, the genus is an ideal subject for a cladistic analysis of adaptive radiation and biogeographic patterns in the Hawaiian Islands. The particular questions that I address in this analysis are as follows: (1) What are the phylogenetic relationships among the Hawaiian taxa based on morphological and anatomical features? (2) What is the most plesiomorphic or basal taxon in the Hawaiian lineage, and what information is available concerning its time and mode of dispersal to Hawai'i? (3) What are the trends of morphological diversification that can be associated with adaptive radiation in the group? (4) How may the biogeographic patterns displayed by Hawaiian *Tetramolopium* correlate with the geologic evolution of the Hawaiian archipelago, that is, does the Hawaiian lineage of *Tetramolopium* follow the general pattern of west-to-east migration down the islands of the archipelago as is found to be the pattern for most taxa discussed in this volume? (5) What are the main patterns of dispersal and speciation in the Hawaiian lineage?

MATERIALS AND METHODS

Taxa

This study includes the 11 recognized species of Hawaiian *Tetramolopium* shown with their sectional delimitation (Lowrey, 1986). Two of the 11 species, *T. conyzoides* and *T. tenerrimum*, are considered extinct, and another, *T. capillare*, has just been rediscovered (S. Perlman, unpubl.). Therefore, for this study these three species have been examined only from limited herbarium material. One species, *T. filiforme*, has previously been suggested to have undergone introgressive hybridization (Lowrey,

1986). Cladograms with and without the inclusion of this species were produced and compared as a test of the validity of the introgressive hybridization hypothesis.

Outgroup

All available biosystematic evidence indicates that the Hawaiian taxa are derived from a single dispersant from New Guinea. Evaluation of herbarium specimens of New Guinean taxa shows that these species also form a cohesive and presumably monophyletic group. Therefore, the New Guinea taxa are here used collectively as the outgroup. In the instances in which the New Guinea taxa are polymorphic for certain characters, they are coded as polymorphisms. Because the focus in this study is on the Hawaiian taxa, the Australian genera that are related to *Tetramolopium* are not used as outgroups. Character data for the New Guinean taxa have been obtained from study of herbarium specimens.

Characters

Twenty-two characters are defined for use in the analysis (Appendixes 11.1 and 11.2). They were chosen based on data derived from the previous biosystematic studies of Hawaiian *Tetramolopium*, including morphological and anatomical analyses. Several characters have multiple states and some are polymorphic in particular taxa. Apomorphic characters for single taxa were not included because they are not phylogenetically informative.

Data Analysis

Cladistic analyses were performed using PAUP version 3.0 (Swofford, 1991) run on a Macintosh IIsx computer. Cladograms were produced using Wagner parsimony. All characters, including multistate ones, were treated as unordered to eliminate bias. The branch-and-bound search option was used to produce the shortest-length cladograms. Different taxon-addition sequences were used, and they all produced identical cladograms. Consensus cladograms were generated using strict and 50% majority rule options. Two sets of cladograms were produced, one including all taxa and one with the deletion of *Tetramolopium filiforme*, a taxon suspected to have undergone intersectional introgressive hybridization as noted above. Area cladograms for biogeographic analysis were

produced by substituting the names of the islands of occurrence for the taxon names on the cladograms.

RESULTS AND DISCUSSION

Phylogeny Excluding *Tetramolopium filiforme*

The phylogenetic analysis produced three equally most-parsimonious trees (Figures 11.2 and 11.3A and B), with 47 character state changes (Figure 11.2) and a consistency index (CI) of 0.87 and a retention index (RI) of 0.90. The strict consensus and 50% majority rule cladograms are shown in Figure 11.3C and D, respectively. In all trees, three distinct clades are resolved, each of which corresponds exactly to one of the morphologically delimited taxonomic sections (Table 11.1 and Figure 11.2). The three trees differ only in the arrangement of taxa within two of the clades. Those differences that result in unresolved polytomies in two of the clades in the strict consensus cladogram (Figure 11.3C) are due to alternative arrangements involving three taxa in each clade. The section *Alpinum* clade, containing *Tetramolopium humile*, is the basal clade in the Hawaiian lineage of *Tetramolopium*.

One of the set of three equally parsimonious trees is presented with labeled character state changes as a basis for discussing major patterns of character state evolution (see Figure 11.2). The basal section *Alpinum* lineage is essentially delimited by having evolved female fertility in the disk florets. The single species of this lineage is also polymorphic for several characters associated with capitulescence type, number of disk florets, and disk floret color (Appendixes 11.1 and 11.2).

The section *Tetramolopium* clade also is defined by synapomorphic characters related to floral features. All taxa of this clade have developed leaf storage parenchyma to some degree. An unusual deflexion of the heads has developed in the taxa, and this character was observed only when the taxa were grown in the greenhouse. Because two of the taxa have not been grown (*T. capillare* and *T. tenerrimum*), it is not known whether they possess this feature. Diversification within the clade is associated with changes in head size and leaf morphology and anatomy. The taxa all have female-sterile disk florets that represent a reversion to the ancestral state.

The section *Sandwicense* clade is defined by a combination of synapomorphies including habit, leaf morphology, and reproductive mor-

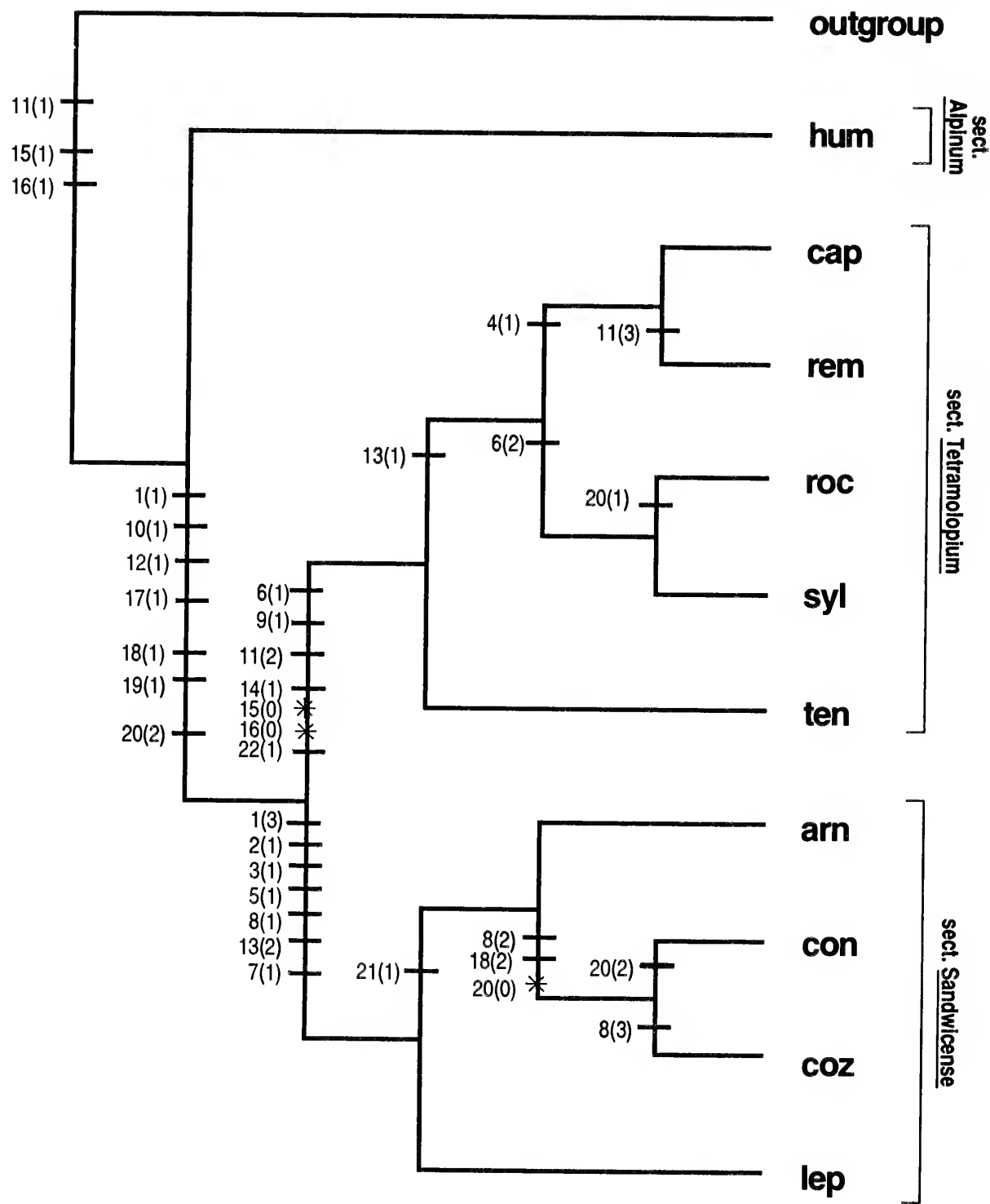


FIGURE 11.2. Preferred cladogram among the three most-parsimonious cladograms excluding *T. filiforme*. The trees are 47 steps long with a CI of 0.87 and an RI of 0.90. Characters are numbered and taxa are abbreviated as in Appendixes 11.1 and 11.2. Correspondence of the taxonomic sections with the clades is shown. Character state changes are included in parentheses next to character numbers; see text for discussion. An *asterisk* indicates a reversal.

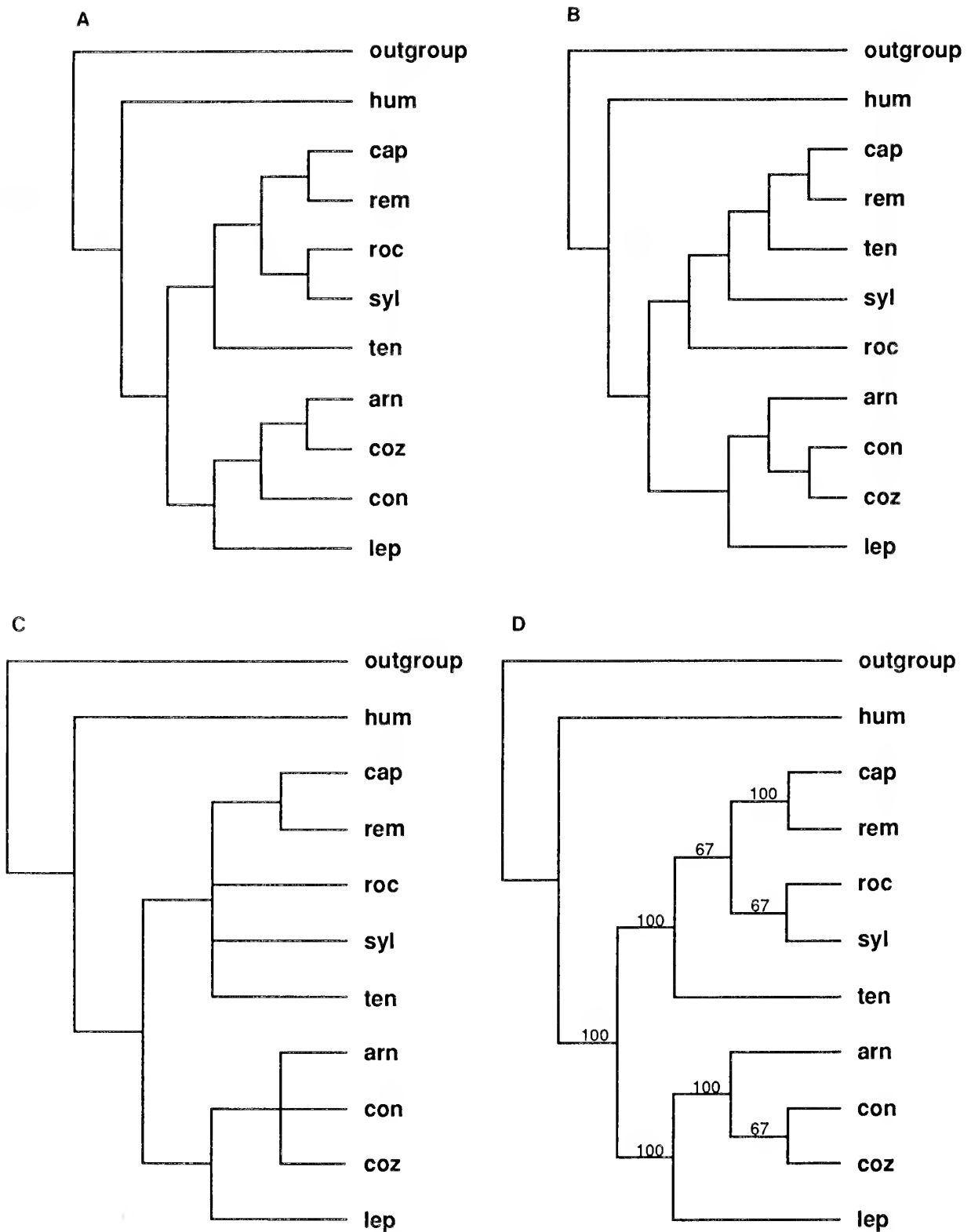


FIGURE 11.3. (A and B) Other most-parsimonious cladograms, in addition to the one shown in Figure 11.2. (C) Strict consensus cladogram for the three equally parsimonious trees of Hawaiian *Tetramolopium* excluding *T. filiforme*. (D) Majority rule consensus cladogram for the three equally parsimonious trees excluding *T. filiforme*. Percent occurrences of clades are listed above horizontal branches. Taxa are abbreviated as in Appendix 11.2.

phology. Speciation within the clade has been accompanied primarily by changes in head number, plant height, and leaf pubescence.

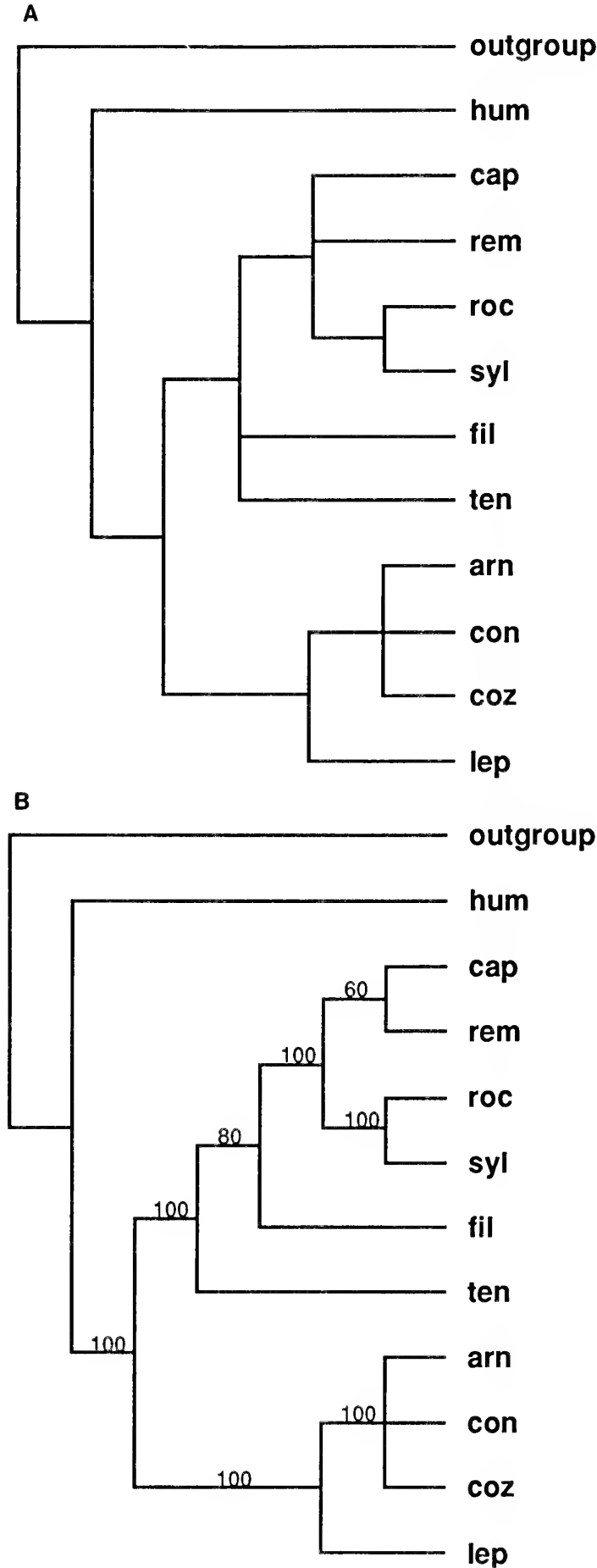
Phylogeny Including *Tetramolopium filiforme*

The phylogenetic analysis when *Tetramolopium filiforme* was included in the data matrix produced 10 equally parsimonious trees with 53 steps and a CI of 0.86 and an RI of 0.87. The strict consensus tree is shown in Figure 11.4A, and the majority rule consensus cladogram is shown in Figure 11.4B. *Tetramolopium filiforme* is included within the section *Tetramolopium* clade in all trees. One of the trees is illustrated with character changes included (see Figure 11.5). Comparison with the cladogram from which *T. filiforme* is excluded (see Figure 11.2) does not reveal any major changes in character evolution when this taxon is added. Basically, inclusion of *T. filiforme* necessitates an extra four steps in the cladogram (reversal in leaf shape and reversal in development of involute leaves). Also, there is a significant increase in the number of most-parsimonious trees generated. However, examination of character states for *T. filiforme* does show polymorphism in two characters that relate to capitulescence structure and disk floret color. All these characters are definitive for separating the clades represented by sections *Tetramolopium* and *Sandwicense*, indicating that *T. filiforme* does combine characters from the two different clades and therefore lending support to the hypothesis suggesting that the taxon has undergone introgressive hybridization.

Phylogeny and Dispersal to the Hawaiian Islands

It is of major interest that *Tetramolopium humile* occurs only in alpine or subalpine habitats on Maui and Hawai'i and therefore occupies an equivalent ecological niche to those in which the New Guinean taxa occur. Organisms in the Hawaiian Islands have originated from ancestors that arrived there via long-distance dispersal, because the nature of the geologic history of the archipelago precludes other possibilities. Carlquist (1981) stressed the point that whether a dispersal event results in successful establishment of an organism in another area depends on the equivalence between the ecology of the source area and that of the recipient area. Paleoecological studies suggest that past climatic conditions in the Pleistocene were favorable for long-distance dispersal between New Guinea and the Hawaiian Islands (Selling, 1948; Flenley, 1979). As

FIGURE 11.4. (A) Strict consensus cladogram of 10 equally parsimonious trees of Hawaiian *Tetramolopium* derived from the analysis of all species including *T. filiforme*. (B) Majority rule consensus cladogram of 10 equally parsimonious trees for all Hawaiian *Tetramolopium* species. Percentage occurrences of clades are listed above horizontal branches. Taxa are abbreviated as in Appendix 11.2.



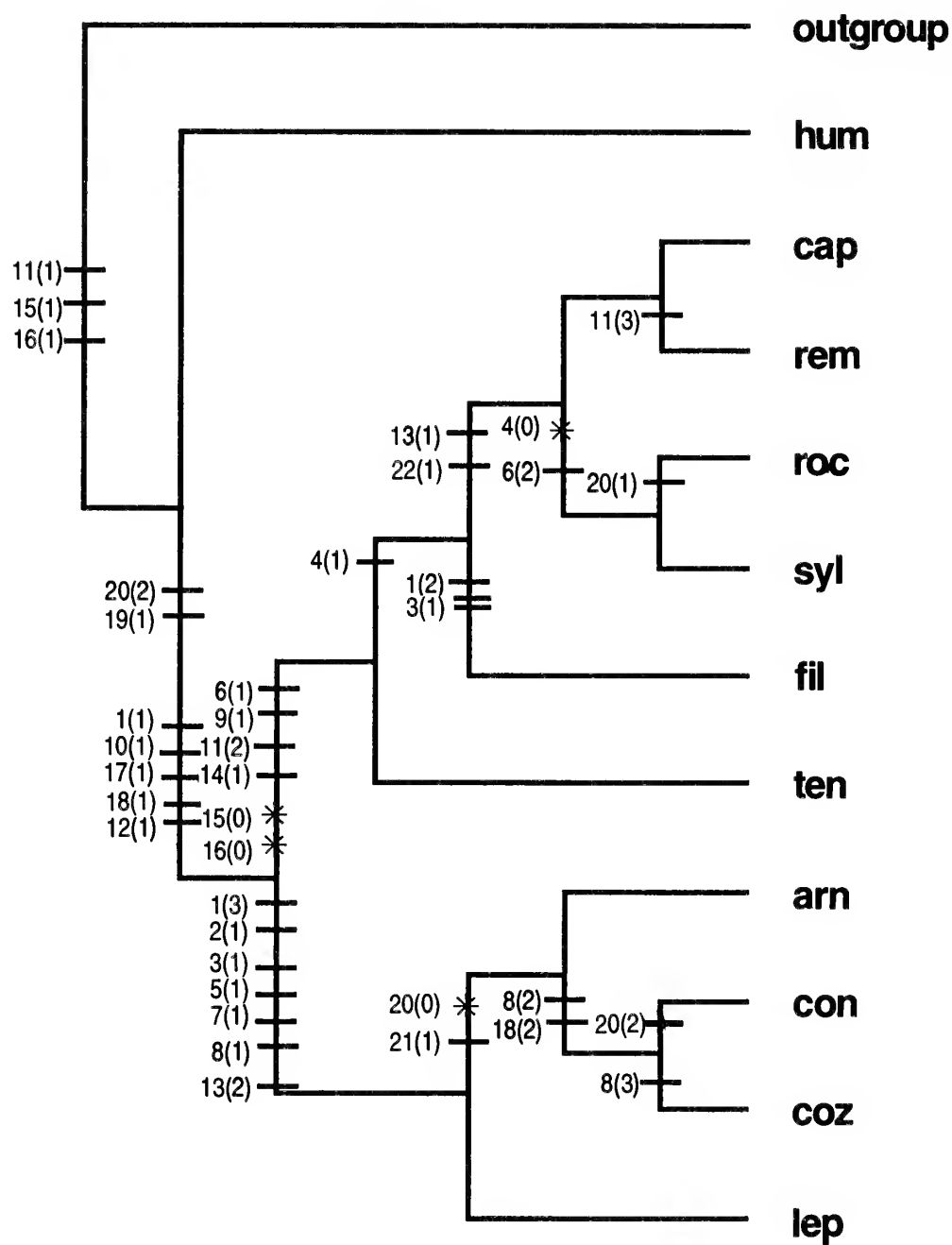


FIGURE 11.5. One of 10 equally parsimonious trees from all the species listed in Table 11.1. The tree is 53 steps long with a CI of 0.86 and an RI of 0.87. Characters are numbered and taxa are abbreviated as in Appendixes 11.1 and 11.2. Character state changes are included in parentheses next to character numbers. An *asterisk* indicates a reversal, and *double lines* indicate parallelism.

mentioned previously, the New Guinean *Tetramolopium* taxa are strictly high montane plants, which occur in the tropic-alpine vegetation zone (Smith, 1977). The tropic-alpine environments are quite recent, having originated during the late Pliocene or early Pleistocene (Smith, 1980). Studies based on analyses of the fossil pollen record in the Pacific indicate that glaciation during the late Pleistocene caused cooler and drier climates than at present (Hope, 1976; Flenley, 1979; Smith, 1980). The most recent glaciation event, which affected Hawaiian biota from 9 to 30 thousand years ago (ka) (Porter, 1979), was particularly pronounced in New Guinea, where the tropic-alpine vegetation greatly increased in extent (Smith, 1977). Flenley (1979) suggested that the expanded area available to many tropic-alpine taxa in New Guinea during this and earlier periods of glaciation could have provided a larger than usual source of propagules for long-distance dispersal to Hawai'i and other areas in the Pacific.

Isozyme electrophoretic data provides the means for estimating time of divergence between species (Nei, 1987) such that it is possible to provide a rough estimate of how long *Tetramolopium* has been in Hawai'i. Nei (1987, Table 9.7, p. 237) relates genetic identity among species and populations to an evolutionary time scale. The two most divergent taxa are *T. humile* and *T. lepidotum*, based on the mean genetic identity of 0.87 between them (Lowrey and Crawford, 1985). Using this genetic identity value, the time of divergence of these species can be estimated as being between 600,000 and 700,000 years before present. During this period, Haleakala on East Maui was in an active stage of orogeny and achieved, about 400 ka, an elevation 1,000 m higher than that of the present day, thereby totaling more than 4,000 m (Macdonald et al., 1983). In comparison, the highest elevation attained by the volcano that formed West Maui was approximately 2,100 m (Macdonald et al., 1983). At the time of its maximal elevation, Haleakala was the tallest mountain in the Hawaiian archipelago. Undoubtedly, it would have presented considerable tropical alpine habitat suitable for colonization by *Tetramolopium* similar to that present on modern-day Mauna Kea and Mauna Loa, which both now have elevations greater than 4,000 m. It is very likely that the original dispersant from New Guinea was first established in alpine habitat on Maui.

The very high genetic similarity among the Hawaiian species (the lowest similarity value exhibited by comparison of *Tetramolopium humile* and *T. lepidotum* is still within the range of conspecific populations in continental areas) strongly suggests that *Tetramolopium* arrived compar-

actively recently on the Hawaiian Islands and subsequently speciated rapidly (Lowrey and Crawford, 1985). It is generally accepted that there has been explosive radiation in the Hawaiian silversword alliance, but the genetic similarities in that group suggest that the silverswords may have been in Hawai'i for 1.5 million years (Witter and Carr, 1988). The silverswords and most of the other taxa discussed in this book have similar biogeographic patterns that support much older original dispersal events than is suggested for *Tetramolopium*.

Further evidence for recent arrival of *Tetramolopium* is provided by the striking morphological similarity of *T. humile* to one extant New Guinea species in particular, *T. alinae* (F. Muell.) Mattf., with respect to several morphological characters. These characters, not found in the other Hawaiian species, are long pappus bristles, fusiform-cylindric cypselas with large capitate glands and dense strigose pubescence, and linear-ob lanceolate densely strigose leaves. The morphological resemblance is so striking that one is tempted to suggest a close relationship. This possibility is currently being investigated.

The unit of dispersal for *Tetramolopium* is the cypselas, including the attached pappus. The phyllaries of all Hawaiian species examined reflex on maturity, thereby presumably assisting in the shedding of the fruits. It is impossible to determine with certainty the actual method of dispersal because we can only observe the result of long-distance dispersal rather than the process itself. Consideration of the possible methods based on the structure of the dispersal unit does support dispersal by two possible agents, wind and birds. As previously stated, the pappus of the New Guinea species as well as that of *T. humile* is well developed. Based on this observation, it is possible to invoke wind dispersal as a possible mechanism, because the Northern Hemisphere jet stream progresses from Southeast Asia to the Hawaiian Islands (Carlquist, 1980). However, Carlquist (1981) suggested that the distance between New Guinea and the Hawaiian Islands is probably too great and the upper air conditions too harsh to favor wind dispersal of flowering plants by this route.

Bird dispersal of *Tetramolopium* via external transport has been proposed by Carlquist (1974). It is highly possible that the occurrence of *Tetramolopium* on the Cook Islands may be due to bird dispersal, perhaps by migrating Pacific Golden-Plover (G. McCormack, unpubl.). Again, the pappus could function by attaching the cypselas to feathers of birds. However, there is another feature of some *Tetramolopium* cypselas that would aid in attachment to birds, including their feet. The enlarged glandular trichomes found on *T. humile* and *T. alinae* make their cypselas

exceedingly sticky. This stickiness is not produced or enhanced by wetting as in *Blennosperma* (Ornduff, 1964), another Asteraceae taxon that has undergone long-distance dispersal elsewhere in the world. The combination of the prominent pappus and glandular trichomes increases the probability of animal attachment leading to dispersal. Although there are no present-day bird migration routes between the Hawaiian Islands and New Guinea, the possibility for at least occasional visitations may have been greater in the past (Carlquist, 1981). Bird and wind dispersal modes do lend themselves to experimentation, and such studies are needed.

Phylogeny and Adaptive Radiation

Adaptive radiation connotes the process by which a monophyletic group of organisms adapts to a broad diversity of habitats (Carlquist, 1974). Adaptive radiation in this sense has been of major importance in the evolution of the three main clades in Hawaiian *Tetramolopium* and therefore diversification at the sectional level. Ecologically, the sectional clades are quite distinct (Figure 11.6A). In comparison to the “ancestral” alpine habitat of section *Alpinum*, section *Tetramolopium* has radiated into open, xeric lowland habitats whereas section *Sandwicense* now occurs in submesic dry forest habitats at middle to low elevations (Figure 11.6A).

Interestingly, *Tetramolopium* is not present in mesic forest or bog habitats in the Hawaiian Islands, although most New Guinean species occur in mesic areas. In comparison to the spectacular radiation of the Hawaiian silverswords, Hawaiian *Tetramolopium* has only been moderately successful in this regard. The lack of *Tetramolopium* species in mesic habitats in the Hawaiian Islands where other indigenous Asteraceae are successful (Wagner et al., 1990) lends support to the hypothesis that the genus is a recent arrival to the archipelago. By the time the initial dispersant arrived in the islands, the wet forest and bog habitats may already have been occupied. The habitats that *Tetramolopium* occupies at the present time can be generally described as pioneer in nature and devoid of a great number of competing species. The habitats are geologically recent for the most part (discussed below) and consist of harsh, generally dry, sparsely vegetated habitats (Lowrey, 1986). For example, *T. humile* often occurs in what would otherwise be completely bare cinder fields on Maui and Hawai‘i; *T. consanguineum* subsp. *leptophyllum* in section *Sandwicense* occurs in ‘a‘a lava fields or in cracks of pahoehoe flows beneath a sparse canopy of *Metrosideros polymorpha*

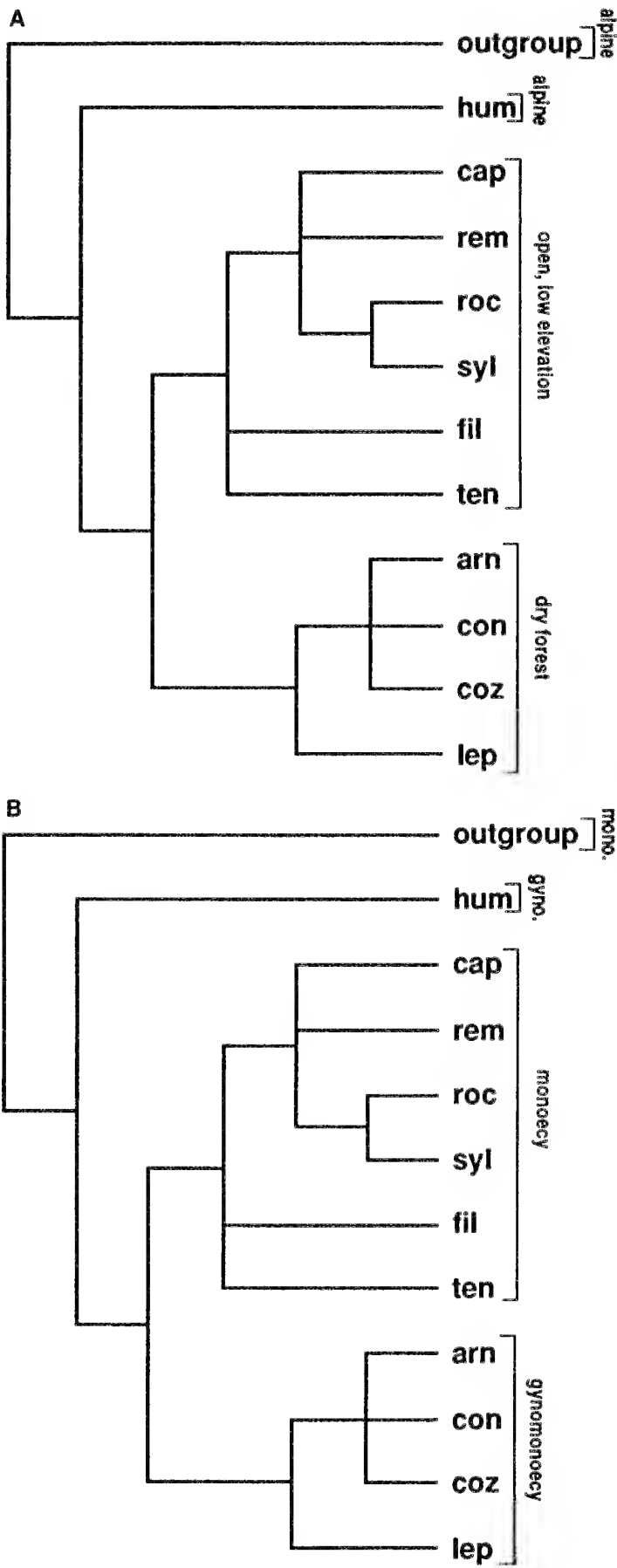


FIGURE 11.6. (A) Strict consensus cladogram (same as Figure 11.4A) with habitat preferences indicated for the outgroup and three main Hawaiian clades. (B) Strict consensus cladogram (same as Figure 11.4A) with sex expressions labeled for the outgroup and three main Hawaiian clades. Taxa are abbreviated as in Appendix 11.2.

Gaud. with few other species present; and *T. rockii* in section *Tetramolopium* occupies dry lithified calcareous sand dune “balds” in company with only three or four other species. Other species of *Tetramolopium* occur in different but similarly harsh environments where only a few hardy pioneer species might be expected to grow. Apparently, *Tetramolopium* taxa are not successful in competition with many other species already established in an area.

In addition to habitat specialization, two other evolutionary trends can be identified in the development of the two clades from the largely plesiomorphic section *Alpinum*: development of upright habit with increasing woodiness, and modification of sex expression (Figure 11.6B) with associated secondary sex characters.

Development of woodiness from herbaceous or nearly herbaceous species that ultimately leads to arborescence is a well-known feature of adaptive radiation in insular plants (Carlquist, 1974). As noted by Carlquist (1974), many cases of increased woodiness involve an ecological shift from open to forest habitats. This is precisely the case for species in the section *Sandwicense* clade, which is defined in part by upright habit and increased stature, both features associated with the development of woodiness. The degree of woodiness spans the range from *Tetramolopium lepidotum*, a small shrub less than 0.5 m high, to *T. consanguineum* and *T. arenarium*, which may attain heights up to 2 m. This range is minor compared with species of woody *Chamaesyce* and *Dubautia* in Hawai'i, but this may well be a function of limited forest habitats available for radiation. *Tetramolopium lepidotum*, the basal species in the clade, now occurs on ridge tops at the very edge of dry forest vegetation in the Wai'anae Mountains on O'ahu. It has been known to occur (now extinct) in dry forest areas on Lana'i and Maui. It may be that *T. lepidotum* now occurs only in marginal habitats that are not a true reflection of its former, much wider distribution. The other three species have all been known to occur as understory species in dry forest habitats. As the species have moved into the understory, their stature has increased, as seen in *T. consanguineum* and *T. arenarium*. It is not known how tall *T. conyzoides* was because it has not been collected for more than 70 years, but judging from branch diameters of available specimens, it may have attained heights of 2 m. In addition to the increase in woodiness, the leaves have increased in length and developed anatomical modifications such as bundle sheath extensions. The adaptive significance of these features is probably related to competition for light in the forest understory. Observations on growth rates of seedlings in the greenhouse

show that species of the section *Sandwicense* clade have much faster growth rates in juvenile stages than do species in other sections.

Much of the reproductive morphological diversity in *Tetramolopium* is attributable to variation in characters associated with the second main evolutionary trend, modification of sex expression. Each sectional clade is consistent for either gynomonoecy (apomorphic) or monoecy (plesiomorphic) (Figure 11.6B) with a particular set of associated characters with varying character states: capitulescence type, disk and ray floret number, head size, disk floret color, and ray floret length. These character suites were termed *syndromes* by Lowrey (1986). The qualitative characters such as capitulescence type and disk floret color are largely invariable within each section (with the notable exceptions of *T. humile* and *T. filiforme*), but the quantitative characters are variable, with particular values for each species. The clade comprising section *Tetramolopium* includes species that are monoecious and have simple capitulescences, yellow disk floret corollas, and larger, more conspicuous heads with greater numbers of florets. The section *Sandwicense* clade comprises species that are gynomonoecious and have maroon disk floret corollas and compound capitulescences, while varying toward a progressively more conspicuous capitulescence with larger numbers of smaller heads, each with fewer florets. Exceptions to these phylogenetic patterns (*T. filiforme*) are polymorphic for capitulescence type and disk floret color. These polymorphisms support the hypothesis that this species has undergone introgressive hybridization that combines features normally found only in one or the other clade. As noted above, *T. humile* of the section *Alpinum* clade is gynomonoecious, yet polymorphic for capitulescence type, disk floret color, and floret number. However, the polymorphism is resolved if the two subspecies are treated independently; each is monomorphic for one or the other state of these characters.

The curious combination of apomorphic and plesiomorphic character states in the sex expression syndromes of sections *Sandwicense* and *Tetramolopium* and the polymorphic nature of some of these characters in *T. humile* may be due to a rare instance in which we are observing the relatively early stages of lineage or phylogenetic sorting of the type suggested for organellar or gene lineages (Avice, 1986; Doyle, 1992). Lineage sorting normally refers to the progressive extinction of organellar (chloroplast or mitochondrial) or nuclear gene lineages following speciation in polymorphic species. We may be seeing the pre-extinction phase of certain character lineages in the polymorphic species (*T. humile*). The alternative hypothesis is that the polymorphisms existing in the section

Alpinum clade have resulted from introgressive hybridization of the sort proposed for *T. filiforme*. Specifically, *T. humile* subsp. *humile* could be the result of past introgressive hybridization with a taxon in section *Sandwicense*. Molecular systematic studies currently in progress in my laboratory and in that of Richard Whitkus at University of California, Riverside, may provide insight into this interesting problem.

The adaptive significance of the sex expression syndromes in Hawaiian *Tetramolopium* is presently unknown. The possibilities include reflection of differences in breeding system (i.e., inbreeding versus outcrossing), pollinator differences, and selection for optimal pollen and seed packaging (i.e., selection for the optimal number of both polliniferous and seminiferous flowers). The limited evidence and arguments for and against these possible adaptive processes are reviewed extensively by Lowrey (1986), and elucidation of the significance of the sex expression syndromes in *Tetramolopium* has not progressed beyond that review.

Hawaiian Biogeography and Speciation

The area cladogram (using the strict consensus cladogram from Figure 11.4A) for Hawaiian *Tetramolopium*, including *T. filiforme*, is shown in Figure 11.7. Members of the genus occur on all main islands except Kaua'i (not included in the map). *Tetramolopium humile*, the basal taxon in the Hawaiian lineage, occurs on the geologically youngest two islands of the archipelago. The species consists of two well-differentiated subspecies: one confined to East Maui (*T. humile* subsp. *haleakalae*) and the other (subsp. *humile*) confined to Hawai'i. The apomorphies possessed by *T. humile* subsp. *humile* are presence of a compound capitulescence, more than one head per branch, and reduced number of disk florets. The latter two characters are a function of producing compound capitulescences (Lowrey, 1986).

Species in the section *Tetramolopium* clade have not been recorded from Hawai'i, but are represented on Maui, Moloka'i, and O'ahu, with only one species, *T. remyi*, occurring on but not endemic to Lana'i. Four of the six species are endemic to single islands. The two taxa endemic to O'ahu, *T. filiforme* and *T. tenerrimum*, occupy basal positions in the clade. Although established taxa in the clade apparently are not extremely mobile within the Hawaiian archipelago, as indicated by the preponderance of single-island endemics, one species, *T. sylvae*, apparently has colonized from the Hawaiian Islands to Mitiaro in the Cook Islands and is in the process of differentiating there (T. Lowrey, unpubl.).

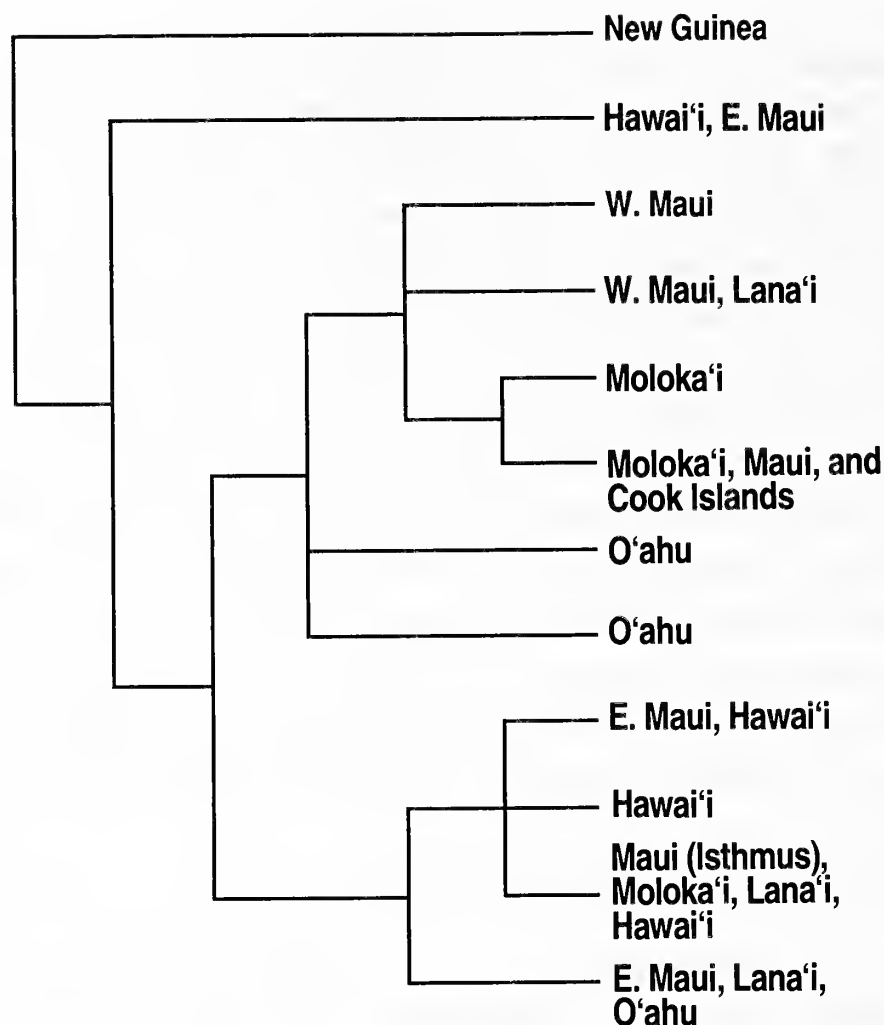


FIGURE 11.7. Area cladogram constructed using strict consensus cladogram from Figure 11.4A.

The taxa in the clade represented by section *Sandwicense* occur on all five of the Hawaiian Islands occupied by *Tetramolopium*. Only one species, *T. consanguineum*, is a single-island endemic, occurring on Hawai'i, and is one of the most derived taxa in the clade. The other three taxa of this clade all occur on Maui and at least one other island.

The results of this analysis clearly indicate that Hawaiian *Tetramolopium* are a major exception to the standard biogeographic pattern in the Hawaiian biota. In sharp contrast to the west-to-east migration pattern followed by most plant and animal groups in the archipelago noted by Carlquist (1980) and reported by contributors in this volume, *Tetramolopium* shows an east-to-west migration pattern in the area cladogram (Figure 11.7). Although the basal taxa of other Hawaiian genera occur primarily on Kaua'i with progressive colonization to the younger islands, the basal taxon (*T. humile*) of *Tetramolopium* is on the youngest islands of Maui and Hawai'i. *Tetramolopium humile* occurs on the geologically youngest portion of Maui (Haleakala, East

Maui) and all the volcanic mountains on Hawai'i, including Hualalai, Mauna Kea, and Mauna Loa. However, it is possible that the original *Tetramolopium* colonist could have been established on West Maui during the Pleistocene and then was dispersed to East Maui with the subsequent extinction of the West Maui population due to habitat change induced by subsidence of the mountain. Most of the remaining Hawaiian taxa are concentrated on the younger islands of the archipelago. However, the section *Sandwicense* and section *Tetramolopium* clades show somewhat different migration patterns (Figure 11.7). In section *Sandwicense*, the basal species in the lineage is *T. lepidotum*, which is recorded from East Maui (Haleakala), Lana'i, and O'ahu. It apparently evolved on East Maui after radiation into dry forest habitat on Haleakala from section *Alpinum* ancestral stock and subsequently dispersed to Lana'i and O'ahu. Currently, it is considered extinct on Maui and Lana'i. The other taxa in the clade were not dispersed to O'ahu. *Tetramolopium arenarium* may represent dispersal downslope into dry forest on the slopes of East Maui (Kula area), followed by speciation and then later dispersal to dry forest areas on Hawai'i (saddle area between Mauna Loa and Mauna Kea). *Tetramolopium conyzoides* perhaps developed in the more xeric dry forest habitat of the isthmus between East and West Maui and then was dispersed from Maui to similar habitats in Moloka'i, Lana'i, and Hawai'i. This is the only taxon in Hawaiian *Tetramolopium* that occurs on all three islands that were once united into the composite island of Maui Nui (Macdonald et al., 1983) in the geologically recent past. Considering the distribution of other taxa in the clade, it appears unlikely that the present distribution patterns can be attributed to vicariance resulting from the breakup of Maui Nui. *Tetramolopium consanguineum* apparently has resulted from a speciation event on Hawai'i, where it is endemic. In summary, of the four species in the clade, three probably evolved on Maui and subsequently dispersed to other islands, whereas the fourth taxon represents a speciation event occurring after dispersal to Hawai'i. This latter speciation event may well be rather recent because this species has not been successfully dispersed beyond Hawai'i.

The biogeographic pattern in section *Tetramolopium* appears to involve back-dispersal from East Maui to O'ahu leading to the development of the semimesic *T. tenerrimum* (leeward Ko'olau Mountains) and the semixerix *T. filiforme* (leeward Wai'anae Mountains). *Tetramolopium filiforme* then may have come into contact with *T. lepidotum*, resulting in a hybridization event that ultimately led to introgression of some character states normally restricted to section *Sandwicense*. Dispersal from East

Maui to dry, open upland areas on West Maui led to the development of *T. capillare* and *T. remyi*, with the latter being dispersed to Lana'i. Dispersal to Moloka'i with radiation into coastal habitats produced *T. rockii* and *T. sylvae*. Geologic evidence supports a very recent origin (15 ka) for *T. rockii*. The Moloka'i lithified dunes on which it occurs and a geologically similar dune system on O'ahu have been the subject of geologic studies (Stearns, 1970, 1973). Stearns (1973) dated the origin of the Moloka'i dunes as 15 ka. The endemism of *T. rockii* to these dunes (and absence on similar dunes on O'ahu and Lana'i) strongly suggests that its progenitor colonized the area 15 ka or less. *Tetramolopium sylvae* has subsequently been dispersed back to Maui (one tiny population on the tip of West Maui).

Tetramolopium on the Cook Islands is represented by one species on the island of Mitiaro. The taxon consists of one population in a narrow strip in the coastal makatea on the eastern side of Mitiaro. Originally I considered this taxon to be conspecific with *T. sylvae* based on limited herbarium material (Lowrey, 1986), but a combination of field observation, cultivation in the greenhouse, and random amplified polymorphic DNA analysis now indicates that it is a distinct and undescribed new species (T. Lowrey and R. Whitkus, unpubl.). However, hybridization studies show that the Mitiaro taxon is fully interfertile with all Hawaiian species but not with New Guinean taxa. Additionally, sequence analysis of the internal transcribed spacer of nuclear ribosomal DNA indicates that the taxon nests within the Hawaiian *Tetramolopium* lineage (R. Chan, T. Lowrey, and R. Whitkus, unpubl.). Therefore, the Cook Island taxon is clearly a close relative of the Hawaiian taxa and has resulted from the dispersal and establishment of a Hawaiian taxon similar to *T. sylvae*.

Generally, the species with the largest number of apomorphic character states have the widest distribution (i.e., they occur on more than one island as shown on the area cladogram) (Figure 11.7). *Tetramolopium sylvae* is the most spectacular example of this phenomenon. In the section *Sandwicense* clade both *T. lepidotum* and *T. conyzoides* occur on at least three islands. However, not all the terminal taxa have wide distributions. An example is *T. consanguineum*, which may represent a very recent speciation event. In fact, the lava flows, which *T. consanguineum* appears to favor, are only several hundred to a thousand years old (R. Shaw, unpubl.). Narrow ecological tolerances and recency of speciation are probably the two main constraints on the distribution of *Tetramolopium* in the Hawaiian Islands. It is quite likely that *T. humile* has dispersed multiple times from Maui and Hawai'i to other islands, but it has not

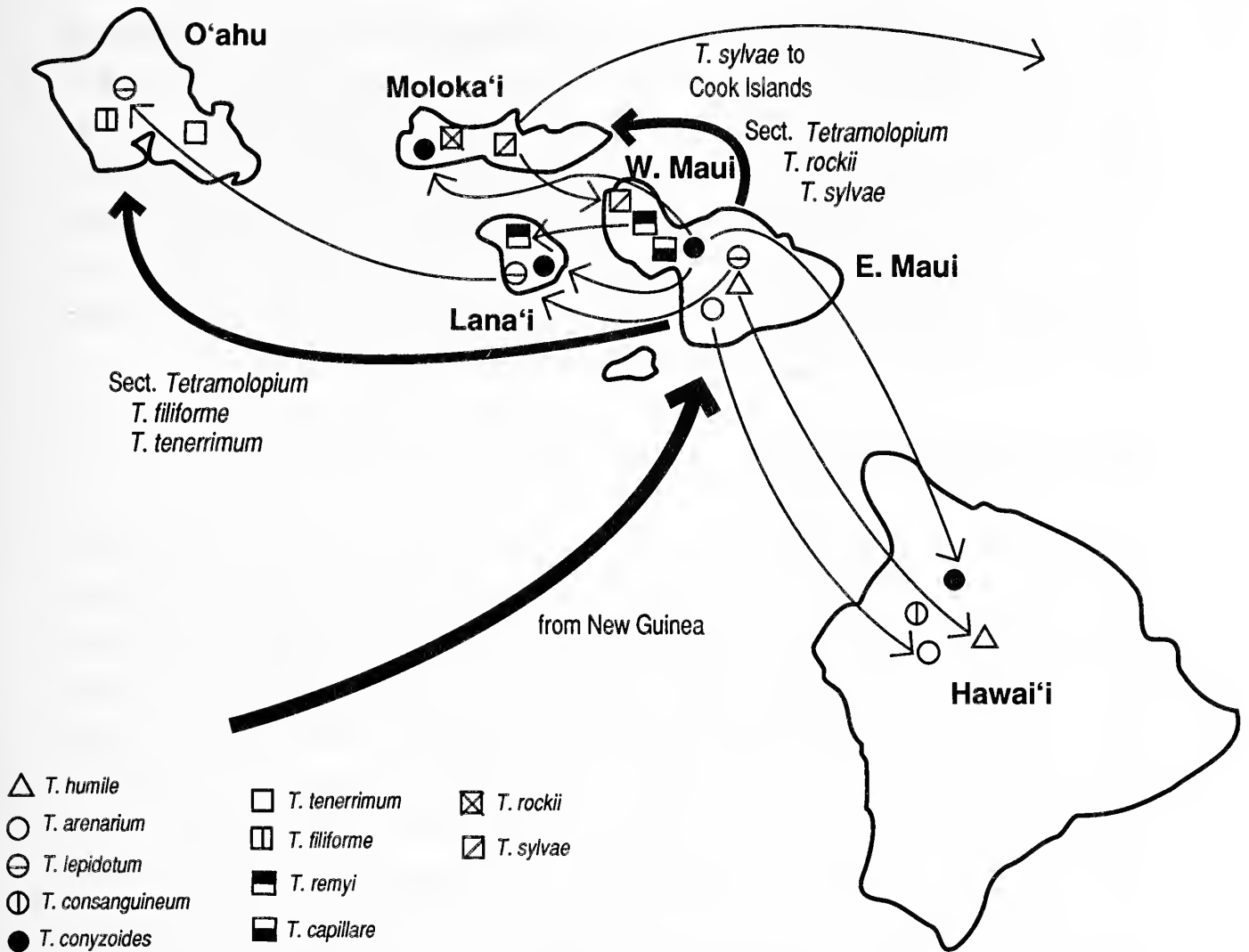


FIGURE 11.8. Distribution pattern of Hawaiian *Tetramolopium*. Thick arrows indicate dispersal of main clades resulting in speciation. Thin arrows indicate inter-island dispersal event of a species. Taxa without lines are assumed to have resulted from a speciation event on the island of occurrence. Triangles indicate the occurrence of taxa in section *Alpinum*; circles indicate occurrence of taxa in section *Sandwicense*; squares indicate occurrence of taxa in section *Tetramolopium*.

successfully become established because tropic-alpine habitats are absent on these islands.

Based on information derived from herbarium records and my own field observations, all species of Hawaiian *Tetramolopium* are allopatric and all occupy different habitats within the general habitat categories of each clade. Therefore, speciation appears to have been largely allopatric and to have resulted from local adaptive radiation after dispersal to a suitable habitat. If species do come into contact, hybridization is possible (e.g., *Tetramolopium lepidotum* and *T. filiforme*), although such contact is rare. The overall distribution pattern is summarized in Figure 11.8. I suggest that this pattern resulted from the survival of a series of founder

dispersal events that began with the establishment of a New Guinean *Tetramolopium* in the tropic-alpine habitat on East Maui or perhaps Maui Nui, followed by many dispersal events and adaptation to other habitats below the alpine zone. The survival of the founders that gave rise to each of the species has been phylogenetically constrained by the ecological tolerances within each clade. The *Tetramolopium* pattern is a striking alternative to the common west-to-east distribution of the other taxa, excepting *Clermontia*, discussed in this volume.

ACKNOWLEDGMENTS

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APPENDIX 11.1. Character List for Hawaiian *Tetramolopium*

1. Habit: 0 = caespitose; 1 = decumbent; 2 = dwarf shrub; 3 = upright.
2. Leaf length: 0 = 1–3 cm; 1 = >3 cm.
3. Leaf shape: 0 = spatulate; 1 = linear to lanceolate.
4. Involute leaves: 0 = absent; 1 = present.
5. Leaf bundle sheath extensions: 0 = absent; 1 = present.
6. Leaf storage parenchyma: 0 = absent; 1 = parenchyma 1–2 cells thick; 2 = parenchyma 3–4 cells thick.
7. Capitulescence: 0 = simple; 1 = compound.
8. Number of heads per capitulum: 0 = 1; 1 = 2–10; 2 = 11–39; 3 = ≥ 40 .
9. Disk floret corolla color: 0 = purple; 1 = yellow.
10. Disk corolla shape: 0 = tubular; 1 = infundibular.
11. Disk floret number: 0 = 10–20; 1 = 1–10; 2 = 20–50; 3 = 50–100.
12. Disk corolla tube length: 0 = 3–7 mm; 1 = 0.6–2.2(–5) mm.
13. Ligule length: 0 = 2.9–4.0 mm; 1 = 4.0–5.0 mm; 2 = 0.7–2.8 mm.
14. Ray/disk floret ratio: 0 = 1–3; 1 = >3.
15. Female fertility of disk florets: 0 = sterile; 1 = fertile.
16. Phyllary number: 0 = 36–70; 1 = 20–35.
17. Pappus length: 0 = 4.1–6.5 mm; 1 = 1.5–4.0 mm.
18. Pappus color: 0 = yellow; 1 = white; 2 = brown.
19. Achene shape: 0 = fusiform-cylindric; 1 = lanceolate-ovoid.
20. Leaf pubescence: 0 = glandular-hispid or glandular-pilose; 1 = glandular-sericeous; 2 = glabrous or short-pubescent.
21. Height: 0 = <0.5 m; 1 = >0.5 m.
22. Peduncles deflexed before anthesis: 0 = no; 1 = yes.

APPENDIX 11.2. Data Matrix of Character States of Hawaiian *Tetramolopium* Species

The characters and character states are defined in Appendix 11.1. Missing data are indicated by question marks, and character numbers separated by a slash (/) indicate polymorphism. The abbreviations in parentheses match the cladogram labels.

| Taxon (abbreviation) | Character | | | | | | | | | | | | | | | | | | | | | |
|-----------------------------------|-----------|---|-----|-----|---|---|-----|-----|-----|----|-----|----|----|----|----|----|----|----|----|-------|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 |
| Outgroup | 0 | 0 | 0/1 | 0/1 | 0 | ? | 0 | 0/1 | 0 | 0 | 0/2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0/1/2 | 0 | ? |
| <i>Tetramolopium humile</i> (hum) | 0 | 0 | 0 | 0 | 0 | 0 | 0/1 | 0/1 | 0/1 | 0 | 0/1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>T. lepidotum</i> (lep) | 3 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 |
| <i>T. conyzoides</i> (coz) | 3 | 1 | 1 | 0 | 1 | 0 | 1 | 3 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 0 |
| <i>T. consanguineum</i> (con) | 3 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 0 |
| <i>T. arenarium</i> (arn) | 3 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| <i>T. capillare</i> (cap) | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | ? |
| <i>T. filiforme</i> (fil) | 2 | 0 | 1 | 1 | 0 | 1 | 0/1 | 0/1 | 0/1 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 0 |
| <i>T. remyi</i> (rem) | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 3 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| <i>T. rockii</i> (roc) | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0/1 | 0 | 1 |
| <i>T. sylvae</i> (syl) | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| <i>T. tenerrimum</i> (ten) | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | ? |

12

Phylogeny and Biogeography in *Schiedea* and *Alsinidendron* (Caryophyllaceae)

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The current Hawaiian angiosperm flora arose from 270 to 282 successful colonization events (Wagner, 1991). In about 10% of these colonization events, spectacular radiations have followed, resulting in morphologically diverse species (Wagner, 1991). These species often occur in strikingly different habitats. Despite the past attention given to these radiations, there have been few attempts to study them from a phylogenetic perspective. A phylogenetic approach provides the opportunity to understand patterns of speciation (inter-island versus intra-island) and the association of habitat shifts with speciation and to examine the causes of breeding system evolution in islands. This chapter is about the fate of the monophyletic lineage comprising the endemic Caryophyllaceae subfamily Alsinoideae. The wide geographic and ecological distribution of this lineage in the Hawaiian Islands, coupled with the extensive range of breeding systems and habit, make it an excellent choice for study of adaptive radiation and biogeographic patterns.

Schiedea and *Alsinidendron* comprise the fifth or sixth largest endemic radiation of species in the Hawaiian angiosperm flora (Wagner et al., 1990; Wagner, 1991), depending on the number of colonizations of *Cyrtandra* (Gesneriaceae). Twenty-six species were recognized in the most recent taxonomic treatment (Wagner et al., 1990) with 22 in *Schiedea* and 4 in *Alsinidendron*. Subsequently, two new *Schiedea* species were discovered on Kaua'i (*S. attenuata* and an unnamed species discovered in mid-1993), and one gynodioecious species (*S. sarmentosa*) was resur-

T A B L E 1 2 . 1 . 1 . Breeding System, Habit, Habitat, and Distribution for Species of *Alsinidendron* and *Schiedea*

| Species | Breeding system | Habit | Habitat | Distribution |
|---|--------------------------------------|-------------------|--|------------------------------|
| <i>Alsinidendron</i> | | | | |
| <i>lychnoides</i> (Hillebr.) Sherff | Hermaphroditic, facultative autogamy | Vine | Wet forest | Kaua'i |
| <i>obovatum</i> Sherff | Hermaphroditic, facultative autogamy | Subshrub | Diverse mesic forest | O'ahu |
| <i>trinerve</i> H. Mann | Hermaphroditic, cleistogamous | Subshrub | Wet forest, diverse mesic forest | O'ahu |
| <i>viscosum</i> (H. Mann) Sherff | Hermaphroditic, facultative autogamy | Vine | Wet forest, diverse mesic forest | Kaua'i |
| <i>Schiedea</i> | | | | |
| <i>adamantis</i> St. John | Gynodioecious | Shrub | Dry shrubland | O'ahu |
| <i>amplexicaulis</i> H. Mann | Hermaphroditic | Unknown | Unknown | Kaua'i (extinct) |
| <i>apokrennos</i> St. John | Gynodioecious | Shrub | Dry cliffs | Kaua'i |
| <i>attenuata</i> W. L. Wagner, Weller & Sakai | Hermaphroditic | Shrub | Diverse mesic forest pockets on cliffs | Kaua'i |
| <i>diffusa</i> A. Gray | Hermaphroditic | Vine | Wet forest | East Maui, Moloka'i, Hawai'i |
| <i>globosa</i> H. Mann | Subdioecious | Suffruticose herb | Dry coastal cliffs | O'ahu, Maui, Moloka'i |
| <i>haleakalensis</i> Degener & Sherff | Dioecious | Shrub | Dry subalpine cliffs | East Maui |
| <i>helleri</i> Sherff | Hermaphroditic | Vine | Wet forest cliffs | Kaua'i |
| <i>hookeri</i> A. Gray | Hermaphroditic | Subshrub | Diverse mesic forest | O'ahu |
| <i>implexa</i> (Hillebr.) Sherff | Hermaphroditic | Subshrub | Mesic forest? | Maui (extinct) |

| | | | | |
|--|----------------|----------------|---|-----------------------------------|
| <i>kaalae</i> Wawra | Hermaphroditic | Perennial herb | Diverse mesic forest, wet forest | O'ahu |
| <i>kealiae</i> Caum & Hosaka | Subdioecious | Subshrub | Dry forest | O'ahu |
| <i>ligustrina</i> Cham. & Schlechtend. | Dioecious | Shrub | Dry shrubland, often cliffs | O'ahu |
| <i>lydgatei</i> Hillebr. | Hermaphroditic | Shrub | Dry shrubland | Moloka'i |
| <i>mannii</i> St. John | Subdioecious | Shrub | Dry ridges in diverse mesic forest | O'ahu |
| <i>membranacea</i> St. John | Hermaphroditic | Perennial herb | Diverse mesic forest | Kaua'i |
| <i>menziesii</i> Hook. | Hermaphroditic | Shrub | Shrubland | Lana'i and West Maui |
| <i>nuttallii</i> Hook. var. <i>nuttallii</i> | Hermaphroditic | Subshrub | Diverse mesic forest | O'ahu |
| <i>nuttallii</i> Hook. var. <i>pauciflora</i> Degener & Sherff | Hermaphroditic | Subshrub | Diverse mesic forest | Kaua'i |
| <i>pubescens</i> Hillebr. | Hermaphroditic | Vine | Diverse mesic forest | O'ahu, Moloka'i, Lana'i, and Maui |
| <i>salicaria</i> Hillebr. | Gynodioecious | Shrub | Dry shrubland | West Maui |
| <i>sarmentosa</i> Degener & Sherff | Gynodioecious | Shrub | Dry forest and shrubland | Moloka'i |
| <i>spergulina</i> A. Gray | Dioecious | Shrub | Cliffs in dry shrubland | Kaua'i |
| <i>stellarioides</i> H. Mann | Hermaphroditic | Subshrub | Diverse mesic forest | Kaua'i |
| <i>verticillata</i> F. Brown | Hermaphroditic | Perennial herb | Soil pockets and cracks on dry coastal cliffs | Nihoa |
| sp. nov. (<i>Perlman</i> 13448) | Hermaphroditic | Subshrub | Mesic forest | Kaua'i |

Note: Assessments based on herbarium, greenhouse, or field observations.

rected from the hermaphroditic *S. menziesii* (Wagner et al., 1994; W. L. Wagner et al., unpubl.).

These two genera are quite diverse in morphology, breeding system, and habitat (Table 12.1). The variation in habit within the two genera is among the most striking in the Caryophyllaceae (Figure 12.1). The species vary from large vines of wet forest to compact shrubs of dry areas, sprawling subshrubs, or even perennial herbs with swollen roots in which the aboveground stems are seasonal. Inflorescence structure encompasses tightly congested inflorescences up to 4 cm long with hundreds of flowers to relatively few-flowered inflorescences up to 1.5 m long with widely distant nodes.

These genera express a wide array of breeding systems (Weller et al., 1990), and detailed studies have focused especially on factors that promote the evolution of dioecy (Sakai et al., 1989; Weller and Sakai, 1990; Sakai and Weller, 1991). Ten species of *Schiedea* have dimorphic breeding systems, including dioecy (pistillate and staminate individuals present in populations), subdioecy (pistillate, staminate, and a few hermaphroditic individuals present in populations), and gynodioecy (pistillate and hermaphroditic individuals present in populations). All dimorphic species occur in dry habitats, whereas species with hermaphroditic breeding systems are largely restricted to more mesic or wet habitats (Weller et al., 1990). Most dimorphic species appear to be wind-pollinated; hermaphroditic species may be insect-pollinated or autogamous (Weller and Sakai, 1990). This information has been used to hypothesize that a scarcity of pollinators in dry, windy environments may have resulted in increased selfing rates, the expression of inbreeding depression, and the spread of male-sterile forms (Weller and Sakai, 1990). Coincident with the evolution of dioecy is the evolution of wind pollination, a second presumed response to loss of pollinators on the very windy cliffs and ridges occupied by most dimorphic species.

Schiedea and *Alsinidendron* have colonized nearly throughout the main islands of the Hawaiian archipelago. Most species are restricted to a single island, but 5 of the 29 species, all in *Schiedea*, occur on more than one island. Species of *Schiedea* are found on six of the eight main islands (Table 12.1). One other species is restricted to Nihoa, an older island northwest of Kaua'i that is the largest island of the leeward chain. In contrast, the four species of *Alsinidendron* are restricted to the two oldest main islands, Kaua'i and O'ahu.

Schiedea and *Alsinidendron* constitute a monophyletic radiation in the Hawaiian archipelago, based on the presence of highly specialized



FIGURE 12.1. Habits of the endemic Hawaiian Alsinoideae showing the great diversity in morphology in selected members of the four main clades. (A to C) *Schiedea membranacea* clade: (A) *S. membranacea*; (B) *Alsinidendron obovatum*; (C) *S. verticillata*. (D and E) *S. nuttallii* clade: (D) *S. diffusa*; (E) *S. nuttallii* var. *nuttallii*. (F) *S. adamantis*. (G) *S. globosa*.

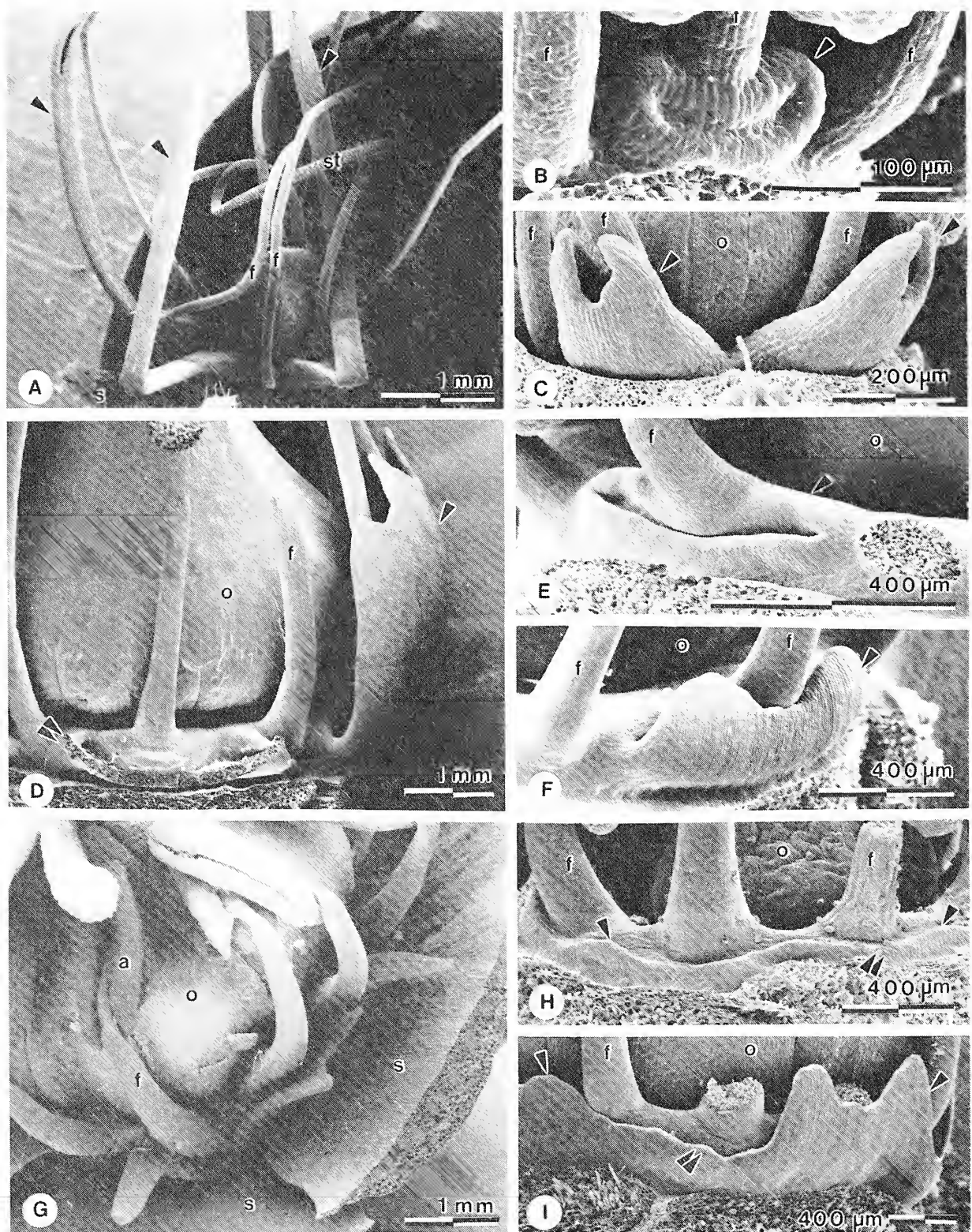


FIGURE 12.2. Stages of nectary development in representative species of *Schiedea* and *Alsinidendron*. Sepals removed in most cases. (A to C) *Schiedea hookeri*. (A) Mature nectaries (arrows) at anthesis. (B) Initiation of nectary at base of filament, inner whorl of stamens (arrow). (C) Early differentiation of nectary as both abaxial and adaxial bulges elongate to form the nectar shaft (arrow). (D to F) *Alsinidendron lychnoides*. (D) Nectary at anthesis consisting of an independent flap derived from the abaxial nectary bulge (single arrow) subtending the nectariferous furrow (flap removed, double arrow). (E) Initiation of nectary (arrow) as in *Schiedea* above. (F) Abaxial portion of nectary elongates to form the independent nectary flap (arrow). (G to I) *Alsinidendron obovatum*. (G) Nectaries forming a fused cuplike structure surrounding the filament bases. (H) Early stages of nectary initiation as elongated bulges (double arrow). After initiation of the nectaries proper, meristematic zones of neighbor-

floral nectaries and the absence of petals in all species. Nectar is collected and presented through a hypodermic-like shaft in *Schiedea* or at the base of a flap- or cup-like structure in *Alsinidendron*. In most members of the subfamily Alsinoideae, to which the endemic Hawaiian genera belong (Pax and Hoffmann, 1934; Weller et al., 1990), the nectary is represented by a mound of nectariferous tissue bisected by a lateral furrow located on the abaxial side of each antesealous stamen (Thomson, 1942).

The monophyletic origin of the endemic Hawaiian Alsinoideae is also supported by ontogenetic studies. These studies indicate that the nectary differences between *Schiedea* and *Alsinidendron* represent changes in homologous structures (E. M. Harris and W. L. Wagner, unpubl.) (Figure 12.2). Moreover, the early stages of initiation and development of nectaries in the Hawaiian genera are homologous to comparable structures of outgroup taxa. The nectaries of *Schiedea* and *Alsinidendron* and the Californian *Minuartia douglasii* (Torr. & A. Gray) Mattf., however, display development beyond the ontogenetic endpoint of the other Alsinoideae, demonstrating a clear-cut case of hypermorphosis (a type of heterochrony; see Funk and Brooks, 1990). Nectary development in the Hawaiian lineage is even more protracted than in *M. douglasii*, yielding a distinctive synapomorphy of the strikingly large nectary appendages.

In this chapter, we use a phylogenetic analysis of the endemic Hawaiian Alsinoideae to examine the importance of island age, inter- versus intra-island colonizations, degree of specialization of successful colonists, habitat shifts, and breeding system modifications as components of speciation. Current distributions of the species are centered on the older islands. In the absence of fossil evidence or a “molecular clock,” we ask whether the phylogenetic hypotheses can be used to differentiate lineages that originally colonized from a continental source directly onto one of the current main islands such as Kaua‘i from those that first colonized, and perhaps even diversified, on older, now-eroded and largely submerged islands (i.e., the leeward chain). We are particularly interested in contrasting patterns found in more highly derived versus more

←
ing nectaries extend and become fused for a more or less continuous nectary meristem (*single arrows*). (I) Growth of nectaries with abaxial flaps (*single arrows*) and internectary region (*double arrow*) elongating differentially, reflecting their respective sequence of initiation. Abbreviations are st, stigmatic surface of style; f, filament; o, ovary; a, anther; s, sepal.

plesiomorphic sublineages. If more highly derived species have become more specialized in morphology and habitat, plesiomorphic sublineages may be more successful at colonizing and diversifying on younger islands. We also examine whether colonization occurs from older to younger islands when habitats become available, as might be expected given the strongly linear pattern of geologic formation of the Hawaiian archipelago. The importance of habitat shifts as well as inter-island dispersal in promoting speciation is also examined. In the case of inter-island founder dispersal, the isolation may be great enough to allow speciation without an accompanying habitat shift. With intra-island dispersal, habitat shifts may be necessary to allow sufficient separation for speciation to occur, especially when dispersal occurs to other parts of the same volcano.

We begin by determining the phylogenetic relationships among the species based on morphological characters. The phylogenetic hypotheses are then used to examine the biogeographic patterns with respect to island age, direction of colonization, biogeographic patterns of specialization and diversification within the lineage, and patterns of habitat and breeding system diversification.

MATERIALS AND METHODS

Selection and Coding of Characters

Forty-two morphological characters were evaluated and studied using herbarium specimens for all taxa, and material of nearly all extant species was grown in the greenhouse (Appendix 12.1) (for detailed discussion of these, see Weller et al., in press b); (0) represents the state found in the generalized outgroup, and (1) or higher represents apomorphic states. Autapomorphic characters were excluded from the analysis. In all cases, outgroup comparison was used to determine the plesiomorphic (0) state. The character state matrix is presented in Appendix 12.2.

Two species of *Schiedea*, *S. amplexicaulis* and *S. implexa*, have not been collected in more than 80 years and appear to be extinct. *Schiedea amplexicaulis* was collected only twice in the early explorations of the archipelago. *Schiedea helleri* was known from only one collection made in 1895 until it was rediscovered in mid-1993. Both *Alsinidendron viscosum* and *S. stellarioides* were also rediscovered during the course of this study. Missing data for several characters of these species, especially of *S. amplexicaulis*, contributed to ambiguity in the phylogenetic hypotheses.

The breeding system of each species, the habitat, and the island distribution (characters 43, 44, and 45) were mapped onto trees but were never used in tree construction. Three additional characters thought to be related to the breeding system, inflorescence condensation (characters 19 and 20) and the ratio of stamen to sepal length (character 35), were eliminated from the analyses presented here because of the likelihood that these characters are homoplasious. The rationale for defining a character as associated with breeding system and the effect of inclusion of breeding system characters on tree topology are discussed in detail in a related paper in which all the characters and their polarizations are described (Weller et al., in press b).

Outgroup Selection

The Caryophyllaceae have the greatest number of species in temperate or boreal regions of the Northern Hemisphere, with only a few tropical representatives (Pax and Hoffmann, 1934; Mabberley, 1987). *Schiedea* and *Alsinidendron* are morphologically divergent within the family. Because of their extensive radiation and great isolation, identification of a continental sister group has proved difficult. McNeill (1962) described *Schiedea* and *Alsinidendron* as aberrant members of the "*Arenaria* complex" but also suggested that these genera might be better placed in subfamily Paronychioidae. The presence of exstipulate leaves, capsules splitting into as many valves as styles, distinct sepals, and the absence of a strophiole on the seed clearly align *Schiedea* and *Alsinidendron* within the subfamily Alsinoideae. The hypermorphosis discussed above in the nectaries of *Alsinidendron*, *Schiedea*, and at least *Minuartia douglasii* and *M. howellii* (S. Wats.) Mattf. of California denote a synapomorphy. Therefore, the latter two taxa were used in this analysis as the most likely sister group to the endemic Hawaiian Alsinoideae. These *Minuartia* species show several specialized features within the genus, such as annual habit. Because of this, we also used a generalized outgroup in the parsimony analyses incorporating the most likely plesiomorphic condition for these characters.

Analysis of the Data Matrix

Phylogenetic Analysis Using Parsimony (PAUP version 3.1.1; Swofford, 1993) was used for analysis. Because of the large number of taxa involved, an heuristic search was performed using the branch swapping

option, MULPARS, and all three search options. The tree bisection-reconnection and subtree pruning-regrafting options yielded the shortest trees (132 steps), whereas the nearest neighbor interchanges gave consistently longer trees. Characters were unordered and unweighted.

Biogeography, habitat, and changes in breeding system were traced on the topologically different trees using PAUP version 3.1.1 (character state reconstruction) and MacClade 3.01 (Maddison and Maddison, 1992). Using PAUP, results from character reconstructions for biogeography, habitat shifts, and breeding system modifications were compared using both accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) optimization options. In character reconstructions, ACCTRAN minimizes and DELTRAN maximizes parallel evolution. PAUP makes no attempt to identify alternative delayed and accelerated transformation reconstructions, and one is selected arbitrarily (Swofford and Maddison, 1992).

RESULTS

Phylogenetic Reconstruction

Six equally parsimonious trees with 132 steps were produced using PAUP (Figure 12.3). The consistency index was 0.508, the homoplasy index was 0.515, the retention index was 0.710, and the rescaled consistency index was 0.360. Tests of confidence were conducted and are presented elsewhere (Weller et al., in press b). Tree topology differed only in the degree of resolution of *Schiedea hookeri*, *S. kealiae*, *S. menziesii*, and *S. sarmentosa* and in placement of the extinct *S. amplexicaulis*. *Schiedea kealiae* was either part of a trichotomy with *S. sarmentosa* and the *S. hookeri* and *S. menziesii* pair or the sister taxon to these species.

In all trees, five clades were present, as shown in the strict consensus tree (Figure 12.4). One clade consisted of the extinct hermaphroditic species, *Schiedea amplexicaulis*, which occurred in three different arrangements (see Figure 12.3), but was never included in the remaining clades. *Schiedea amplexicaulis* was placed either as the sister taxon to all other *Schiedea* and *Alsinidendron* species or as the sister taxon to all clades but the basal one or in an unresolved trichotomy (see Figure 12.3). Placement of this species in its own clade is problematic, largely because so much character information is missing. The only two collections are fragmentary, made during the early exploration of the Hawaiian Islands,

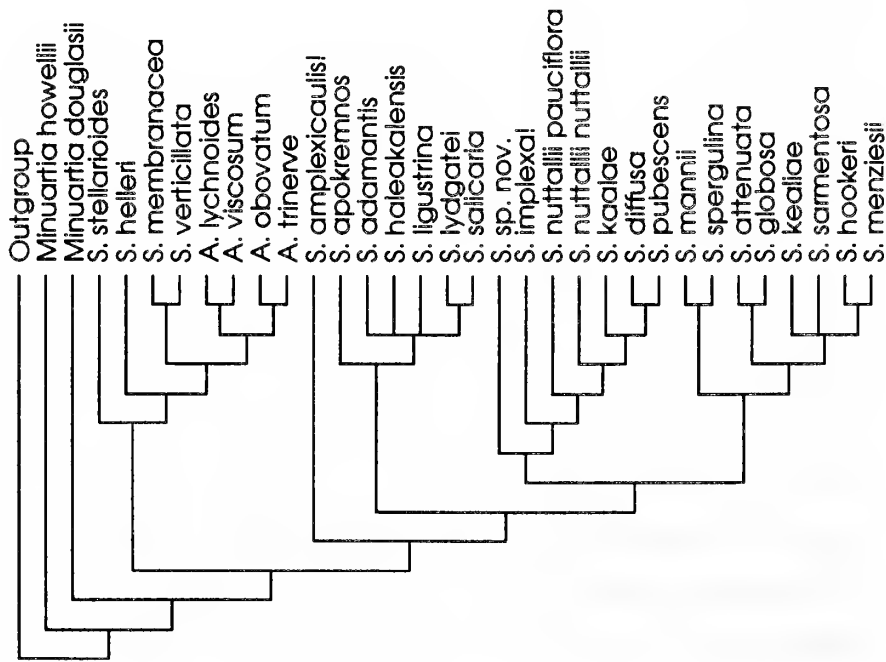
and do not provide the information available for the other species. Unless this species is rediscovered, it is unlikely that a satisfactory phylogenetic placement of it will be possible. Because of this, we will focus only on the four clearly defined clades.

A second, basal clade (the *Schiedea membranacea* clade) consisted of the four species of *Alsinidendron*, *S. verticillata* from Nihoa, and three morphologically divergent Kaua'i species of *Schiedea*. Species in this clade are characterized by broad, multinerved leaves with ciliate or toothed margins. Hermaphroditic breeding systems occur throughout the clade, although these range from cleistogamy (*A. trinerve*) to species that appear adapted to bird pollination but facultatively self-pollinate (*A. lychnoides*) and species that regularly outcross, probably via insects (*S. membranacea*).

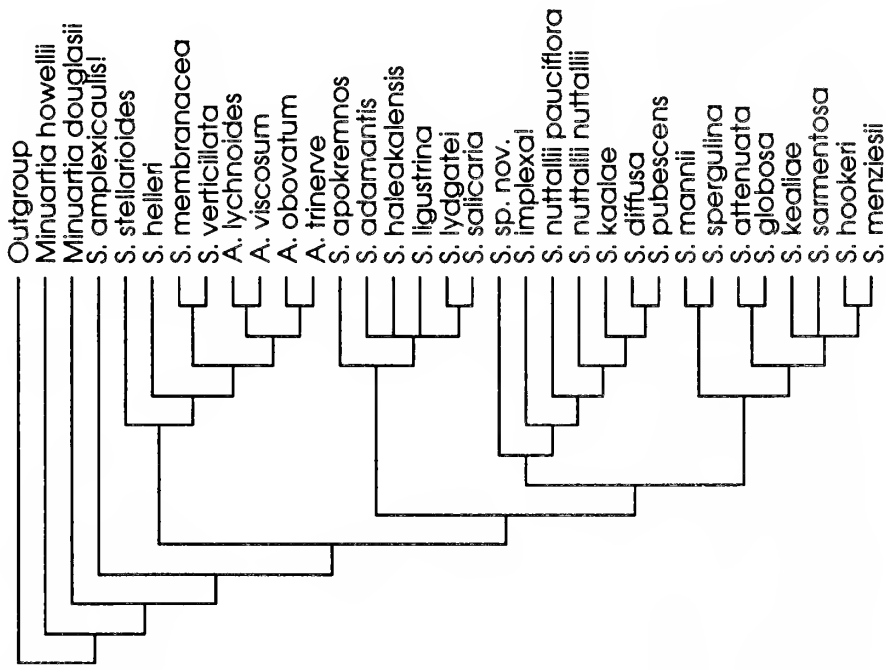
The basal *Schiedea membranacea* clade differs from the other three main clades in the greater degree of morphological diversity, the greater specialization among the constituent species, and the biogeography of these species. In addition to the considerable morphological differentiation between *Schiedea* and *Alsinidendron*, *Schiedea* species of this clade range from fleshy-rooted, herbaceous perennials with broad multinerved leaves (*S. verticillata* and *S. membranacea*) to large vines (*S. helleri*) and small upright subshrubs with single-nerved leaves (*S. stellarioides*). Overall, species in the *S. membranacea* clade are more specialized than those occurring in other clades, as demonstrated by the phylogram in Figure 12.5, in which branch lengths reflect the number of derived characters. This pattern is likely to result from extinctions in the *S. membranacea* lineage, which place more of the synapomorphies on single branches. Species of this clade are more divergent from the remaining three clades than these clades are from each other. The greater degree of differentiation is likely to result from the older age of the *S. membranacea* clade. Despite the morphological diversity, all species in this clade except *S. verticillata* occur in mesic or wet habitats.

The third clade (the *Schiedea adamantis* clade) is morphologically coherent. It consists of six species characterized by narrow coriaceous leaves broadest above the middle and, for all the species except *S. apokremnos*, papillate seeds and acute cell margins on the cells of the testa. All species are shrubs occurring in dry habitats, ranging from near sea level (*S. adamantis*) to dry subalpine cliffs (*S. haleakalensis*). Several species (*S. adamantis*, *S. haleakalensis*, *S. ligustrina*, and the branch with *S. lydgatei* and *S. salicaria*) are so similar that they form an unresolved polytomy in all trees (see Figure 12.3). They are distinguished primarily

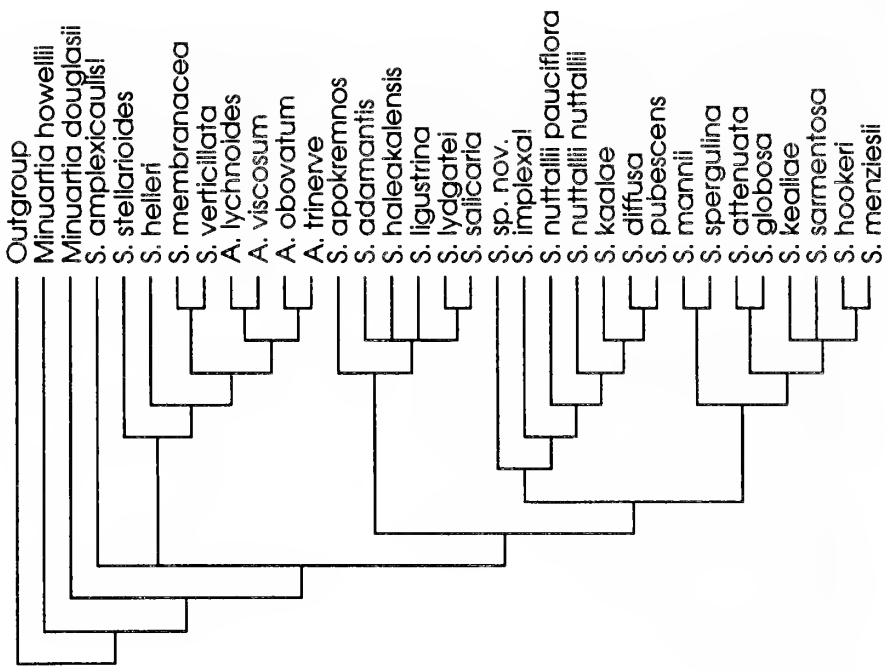
1



2



3



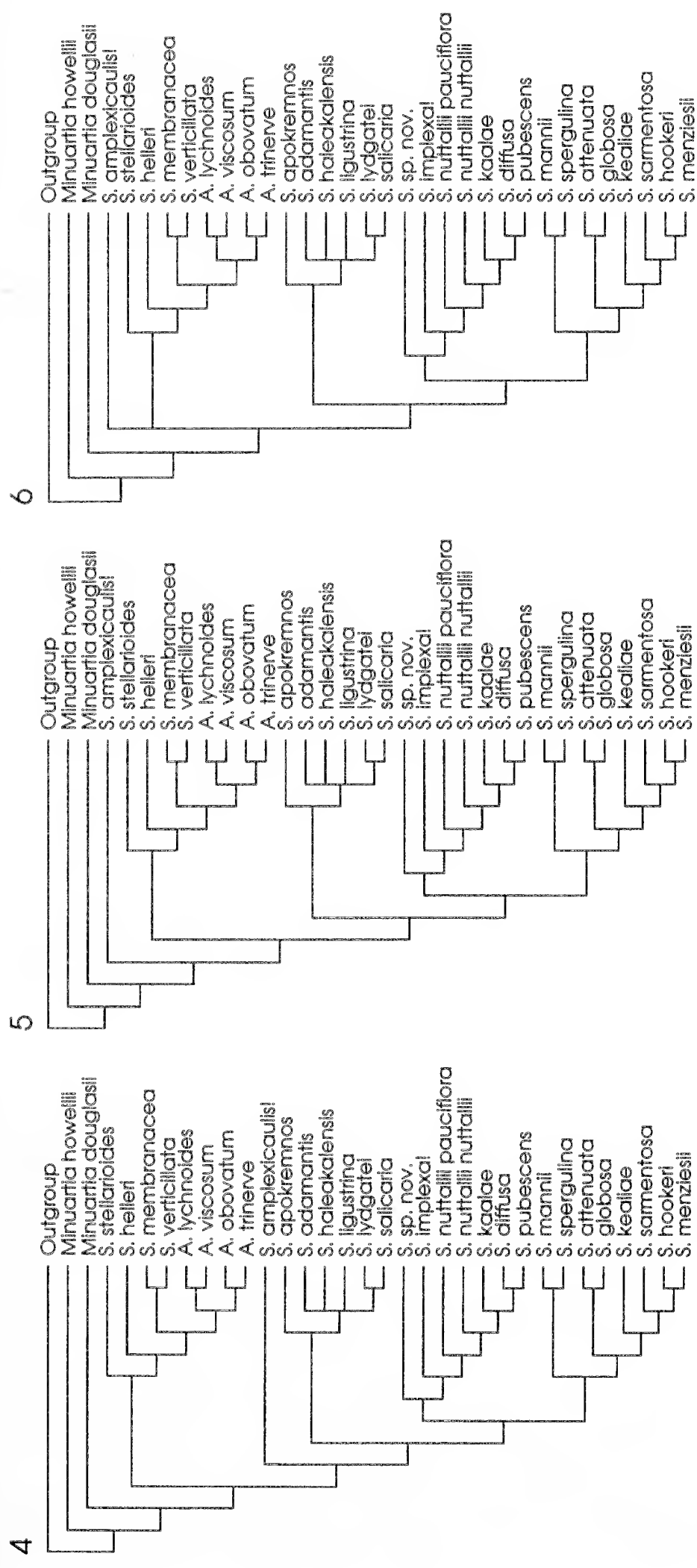


FIGURE 1 2 . 3 . Six equally parsimonious trees obtained from the PAUP analysis. An *exclamation mark* indicates an extinct species. Tree 4 is the preferred tree.

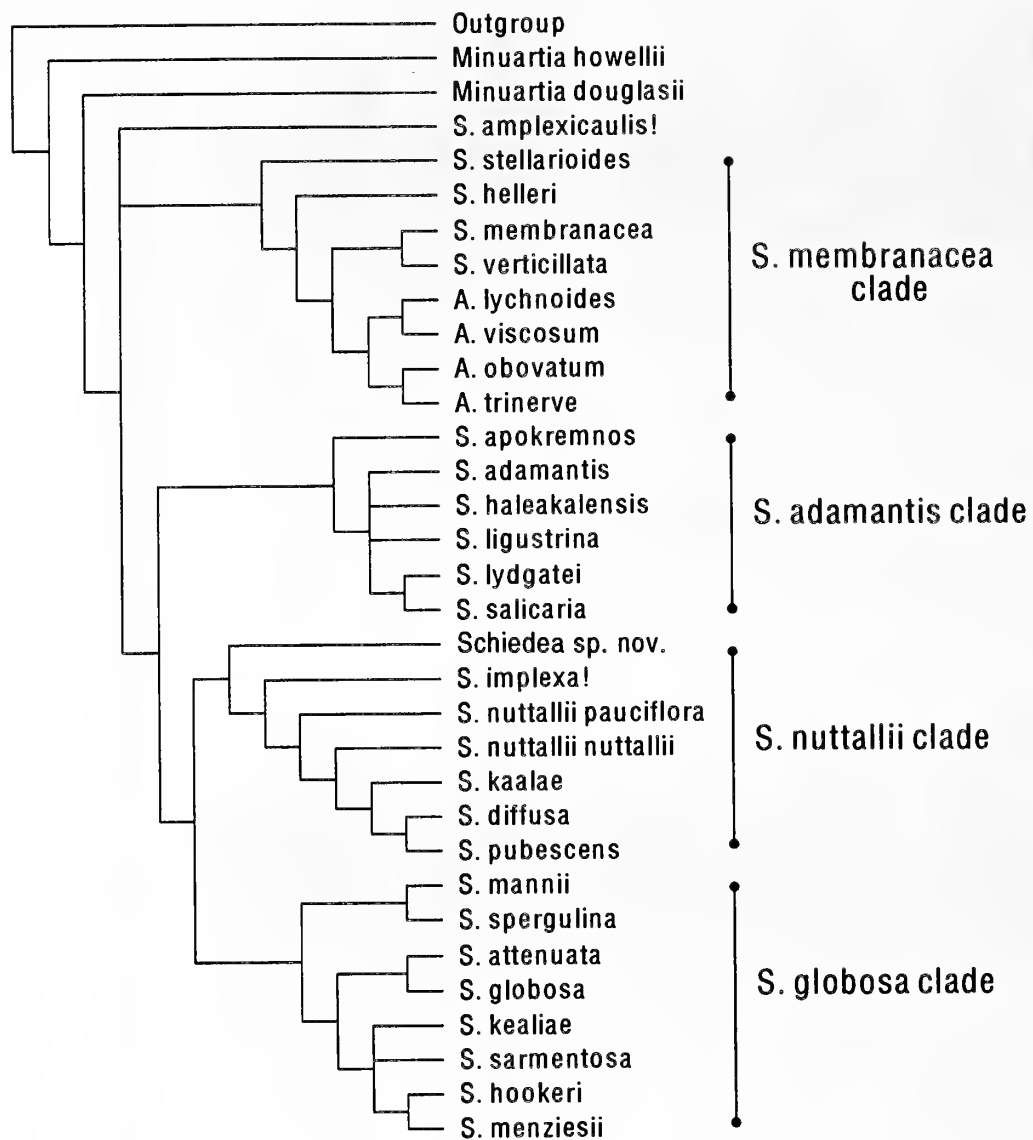


FIGURE 12.4. Strict consensus tree of six most-parsimonious trees for *Schiedea* and *Alsinidendron* shown in Figure 12.3. Tree length is 132 steps. The four main clades are named for characteristic species. An *exclamation mark* indicates an extinct species.

by differences in breeding systems and the degree of inflorescence condensation, characters that were not used in phylogenetic analysis. The divergent species in this clade, *S. apokremnos*, lacks the specialized seed traits characteristic of the other species in the clade. It possesses several unique features including glaucous leaves and occasionally globose inflorescences, and it apparently diverged early in the evolutionary history of the clade. All species in this clade except *S. lydgatei* have dimorphic breeding systems. Although species in this clade occur on five of the eight main islands, they are most diverse on O'ahu and the Maui Nui complex.

A fourth clade (the *Schiedea nuttallii* clade) has six species and is uniformly distinguished from the other clades by large, single-nerved

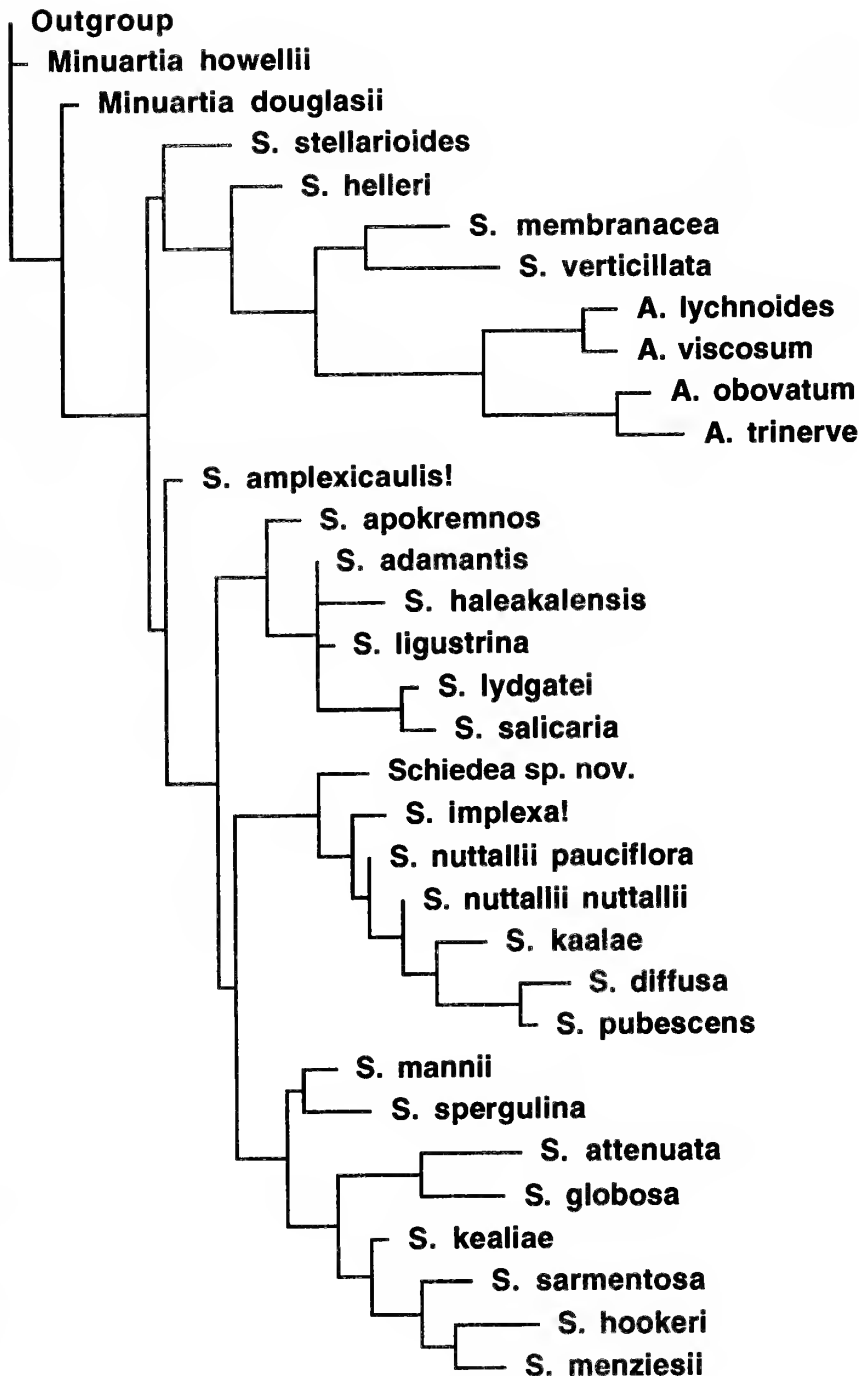


FIGURE 12.5. Phylogram of the preferred tree for *Schiedea* and *Alsinidendron* in which branch lengths reflect the number of derived characters, showing that the species in the *S. membranacea* clade are more specialized than those occurring in other clades. An *exclamation mark* indicates an extinct species.

leaves (except the undescribed species, which has three-nerved leaves) and distinctive attenuate to caudate, strongly reflexed sepals. *Schiedea implexa* and the undescribed species from Kaua'i lack the ciliate sepals typical of the remaining taxa, and for that reason, they occur in the basal positions in the clade. All species of this clade occur in mesic or wet habitats and possess hermaphroditic breeding systems. One species, *S. diffusa*, is apparently autogamous. Seeds of this species are retained in

the capsule and germinate in situ. The *S. nuttallii* clade is the most widely distributed of the five clades, occurring on six of the eight main islands.

A fifth clade (the *Schiedea globosa* clade) consists of eight species with narrow attenuate, asymmetric or falcate, and, in most cases, several-nerved leaves. Species in the *S. globosa* clade are shrubs and subshrubs occurring in mesic to dry environments, primarily on O'ahu, Maui, and Moloka'i. The degree of variability within this clade is similar to that found in the *S. adamantis* and *S. nuttallii* clades but far less than the variability in the *S. membranacea* clade (Figure 12.5). Breeding systems are diverse, with three hermaphroditic species (two of which occur in mesic environments) and five dimorphic species (all of which occur in dry habitats).

Three of the four main clades (all but the *Schiedea globosa* clade) are reasonably well supported, based on bootstrap and decay analysis (Weller et al., in press b). Molecular data (restriction analysis of chloroplast DNA and 18–26S rDNA) provide support for the same three clades (D. Soltis et al., unpubl.). The *S. globosa* clade, which is delimited by a single morphological synapomorphy, is not supported in the bootstrap analysis or from molecular data and may well represent a grade rather than a clade.

Biogeographic Patterns

Using PAUP with the ACCTRAN option, biogeographic analysis of all equally parsimonious trees indicates that all but one clade originated on Kaua'i (Figure 12.6). An O'ahu origin is suggested for the *Schiedea globosa* clade. The PAUP analysis indicates that most colonization events occurred from older to younger islands, and many were associated with speciation. There were 18 hypothesized colonizations from older to younger islands, 11 resulting in speciation and 7 occurring without speciation. Four back-colonizations from younger to older islands are hypothesized, three resulting in speciation and one that did not result in speciation. Thus, almost two-thirds (11 of 18) of the colonizations from older to younger islands resulted in speciation. The three back-colonizations resulting in speciation are *S. verticillata* on Nihoa from a Kaua'i ancestor and *S. attenuata* and *S. spergulina* on Kaua'i from different O'ahu ancestors. A back-colonization by *S. pubescens* is hypothesized, which did not result in speciation. Five of eight inter-island colonization events that occurred without speciation took place within the Maui Nui complex.

Using the DELTRAN option, the origin of the *Schiedea globosa* clade occurs on Kaua'i. If the origin of the *S. globosa* clade was on Kaua'i,

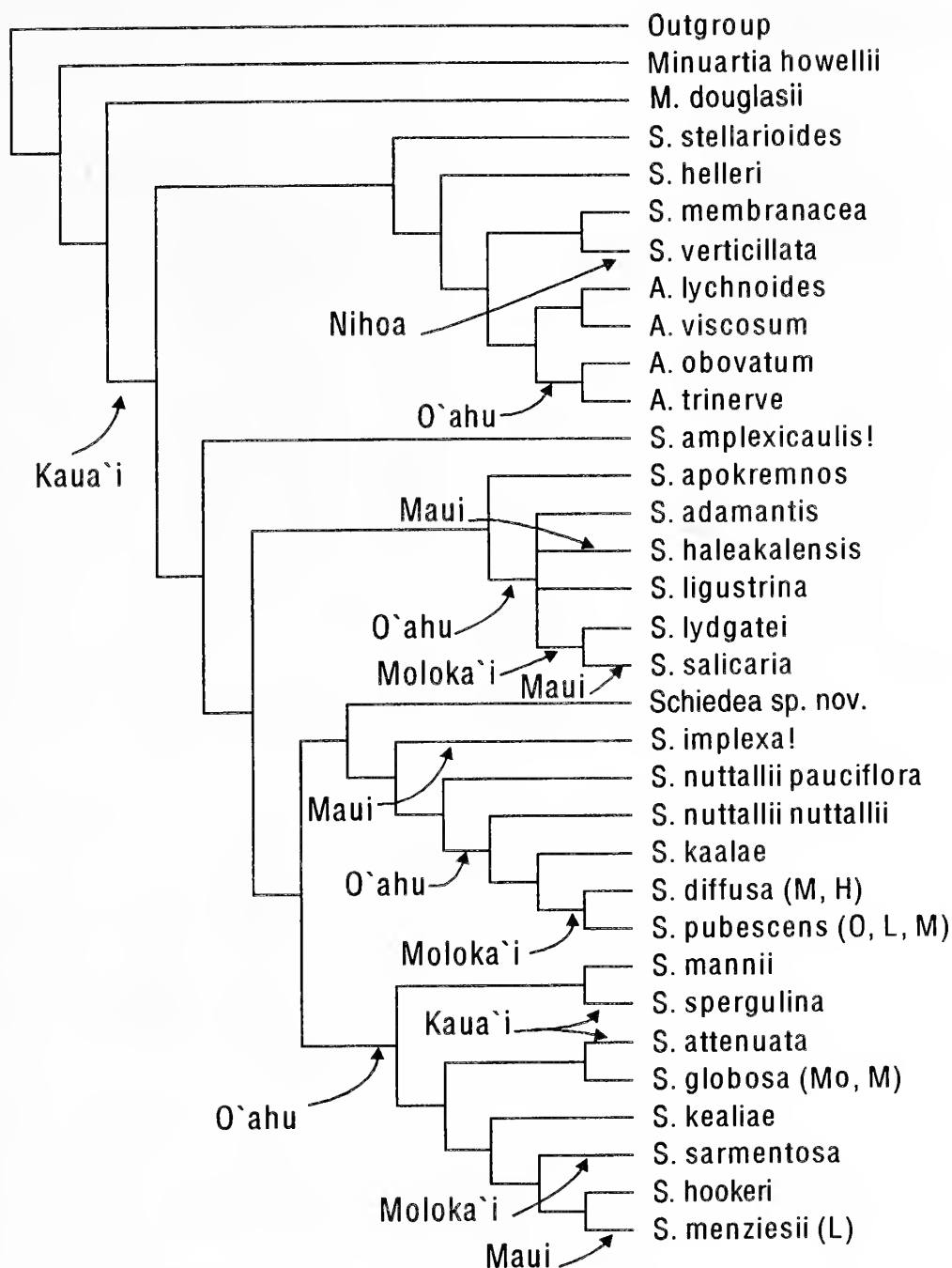


FIGURE 12.6. Biogeographic hypothesis for *Schiedea* and *Alsinidendron* mapped onto preferred tree using PAUP and the ACCTRAN option for character reconstruction. An *exclamation mark* indicates an extinct species. Colonizations resulting in speciation are shown on the tree; for those colonizations that did not result in speciation, the additional islands on which they occur are indicated next to the species as the first or first two letters of the island name. Both categories include colonizations from older to younger islands and back-colonizations. Eighteen hypothesized colonizations from older to younger islands occurred. Of these, 11 resulted in speciation; the remaining 7 colonizations occurred without speciation. Four back-colonizations are hypothesized; three of these resulted in speciation and one (for *S. pubescens*) did not. Using the DELTRAN option, however, three of the four back-colonizations (all but *S. verticillata*) are interpreted as colonizations from older to younger islands. Note that PAUP gives an arbitrary solution for the common ancestor of the *Schiedea lydgatei*–*S. salicaria* pair. Stepping-stone colonization from O'ahu (O) to Moloka'i (Mo) for the ancestor, followed by colonization to West Maui, may have occurred because of the Pleistocene connection of Maui (M) and Moloka'i. H, Hawai'i; L, Lana'i.

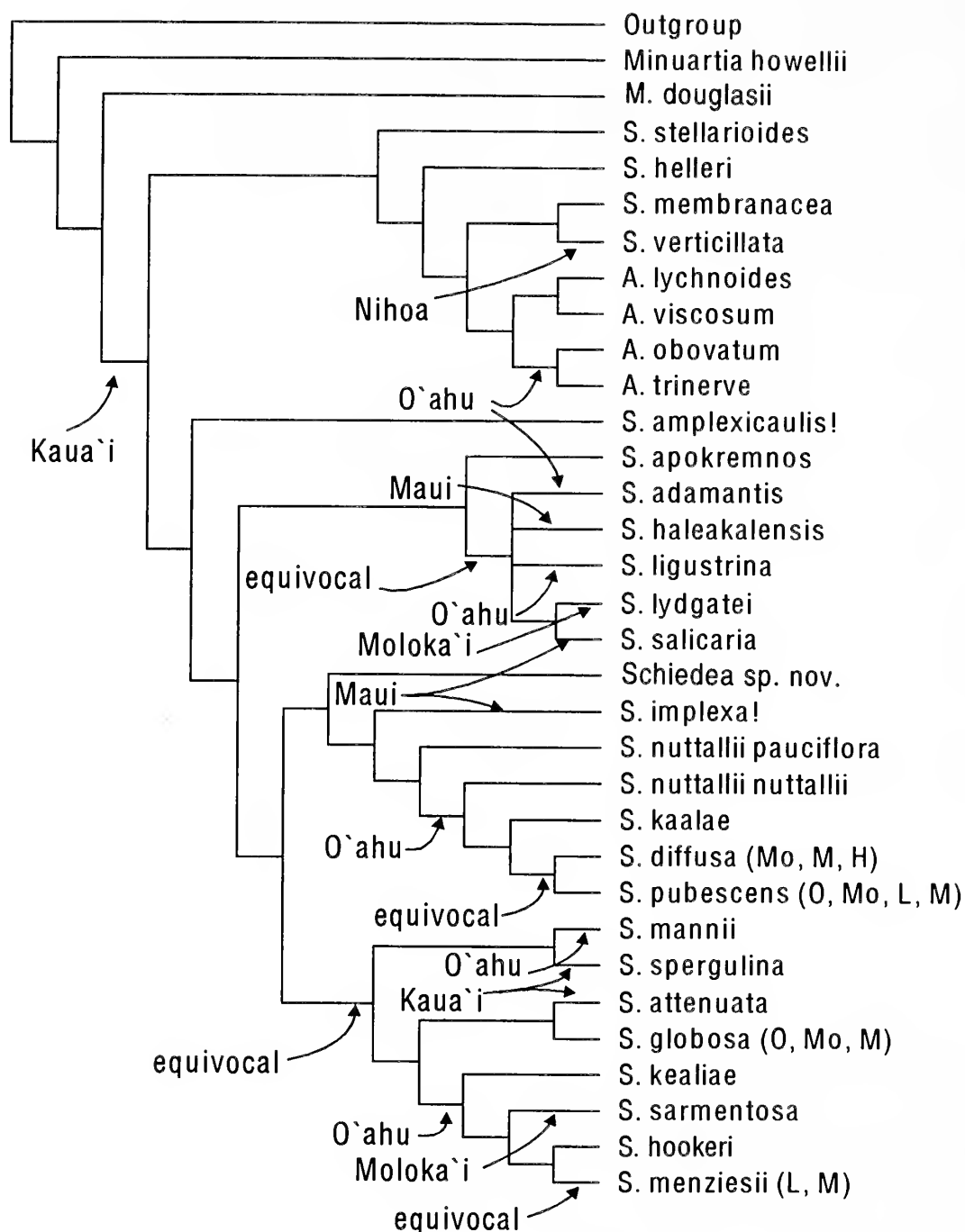


FIGURE 12.7. Biogeographic hypothesis for *Schiedea* and *Alsinidendron* mapped onto preferred tree using MacClade. Origin of the *S. globosa* clade is equivocal and may have occurred on Kaua'i or on O'ahu (O). If the origin of this clade was on Kaua'i, no back-colonizations are necessary to explain the distribution of *S. spergulina* and *S. attenuata*. Using MacClade, the origin of the *S. diffusa*–*S. pubescens* clade is also equivocal, and a hypothesized back-colonization for *S. pubescens* to O'ahu is no longer necessary. Species with multiple-island distributions (*S. diffusa*, *S. globosa*, *S. menziesii*, and *S. pubescens*) are interpreted as equivocal using MacClade. Their distributions are indicated as in Figure 12.6. M, Maui; Mo, Moloka'i; L, Lana'i; H, Hawai'i.

back-colonizations would not be necessary to explain the origin of *S. spergulina* and *S. attenuata* on Kaua'i, and colonization concomitant with speciation would be necessary to explain the origin on O'ahu of *S. globosa*, *S. mannii*, and the ancestor of *S. hookeri*, *S. kealiae*, *S. menziesii*, and *S. sarmentosa*. Another difference using DELTRAN is an O'ahu rather than a Moloka'i origin for *S. pubescens*, thus eliminating another hypothesized back-colonization. Using MacClade to trace characters (Figure 12.7), differences from the PAUP analysis include the equivocal origin of the *S. globosa* clade, which could have been on O'ahu or Kaua'i, and the equivocal origin of the polytomy including *S. adamantis*. The biogeography of four of the five species with multiple-island distributions is interpreted as equivocal by MacClade because terminal taxa are viewed as polymorphic.

Habitat Shifts

Using PAUP, a major habitat shift from a mesic ancestor to dry, often cliff habitats is suggested in the common ancestor of the *Schiedea adamantis*, *S. globosa*, and *S. nuttallii* clades (Figure 12.8). A reversal to mesic habitats occurred in the ancestor to the *S. nuttallii* clade, followed by progressive adaptation to wetter habitats within the clade. Adaptation to wet environments also appears to have occurred in *Alsinidendron* independently on both Kaua'i and O'ahu and in *S. helleri* on Kaua'i. Within the *S. globosa* clade, two additional reversals to mesic habitat have occurred in *S. attenuata* and *S. hookeri*. Adaptation to dry coastal cliffs has occurred independently in *S. verticillata* and *S. globosa*.

Using MacClade to trace habitat shifts, the status of the common ancestor in the archipelago is equivocal and could have been either mesic or dry (Figure 12.9). If the common ancestor occurred in a dry habitat, the only other difference from the PAUP analysis would be the extra shift to a mesic environment in the ancestor of the *Schiedea membranacea* clade. If the basal habitat condition was mesic, the analysis is either identical to the results obtained from PAUP or, alternatively, because of equivocal results, there could have been up to four independent shifts to dry habitats, once for the ancestor of the *S. adamantis* clade and three times within the *S. globosa* clade.

Breeding Systems

Character reconstruction of breeding systems using PAUP indicates that dimorphism has evolved in two of the four main clades (Figure 12.10A).

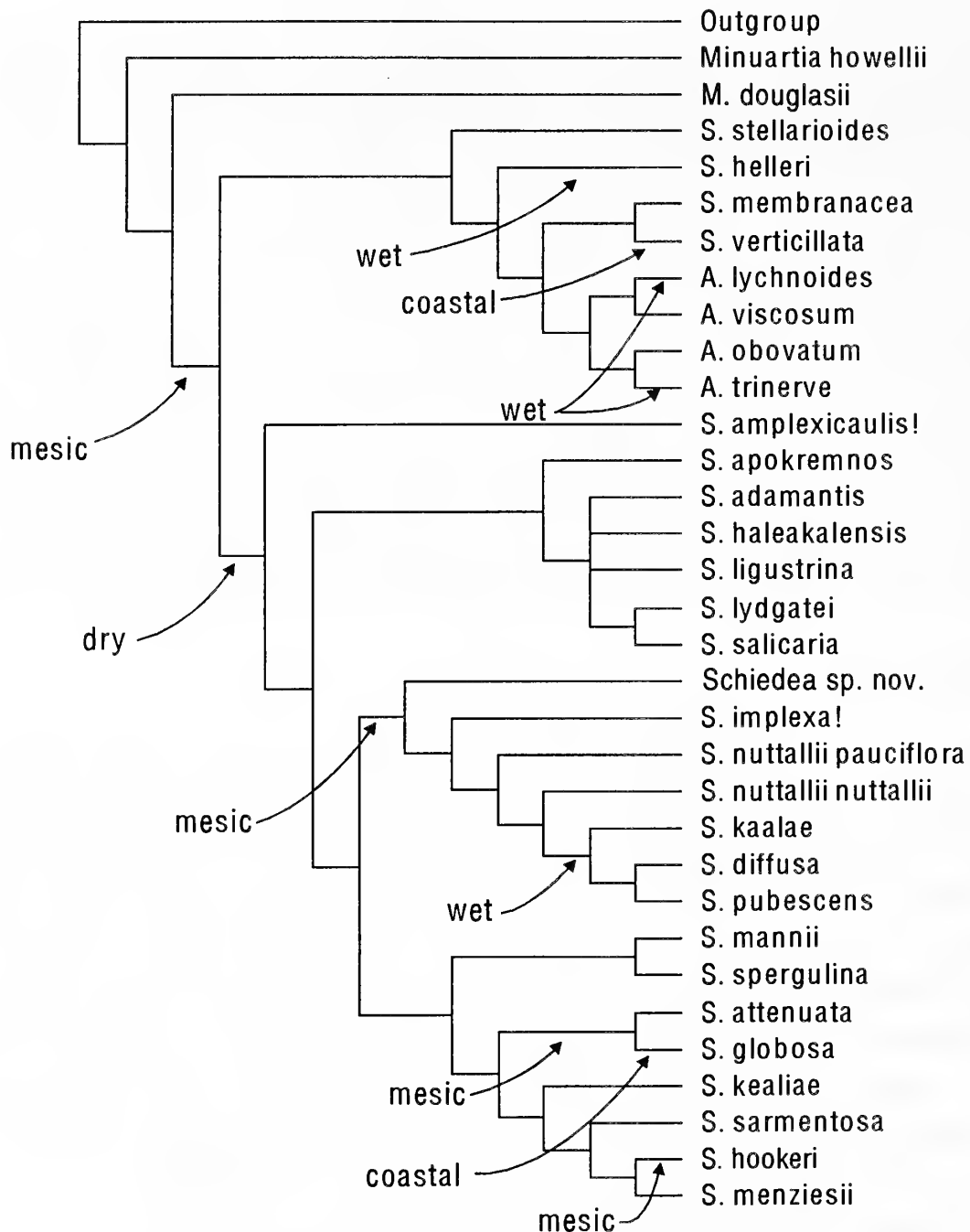


FIGURE 12.8. Hypothesis of habitat shifts in *Schiedea* and *Alsinidendron* mapped onto preferred tree using PAUP character reconstruction and the ACCTRAN option. An *exclamation mark* indicates an extinct species. A major shift from mesic to dry habitat is suggested in the common ancestor of the *S. adamantis*, *S. globosa*, and *S. nuttallii* clades, followed by a reversal to mesic habitats in the ancestor of the *S. nuttallii* clade. Coastal habitats are dry. Note that PAUP gives an arbitrary solution for the common ancestor of the *S. attenuata*–*S. globosa* pair.

Using both ACCTRAN and DELTRAN, gynodioecy is basal in the *Schiedea adamantis* clade, for which the topology is invariant in all six equally parsimonious trees. Using the ACCTRAN option, the number of times dimorphism has evolved in the *S. globosa* clade varies depending on which of two phylogenetic hypotheses most closely represents the course

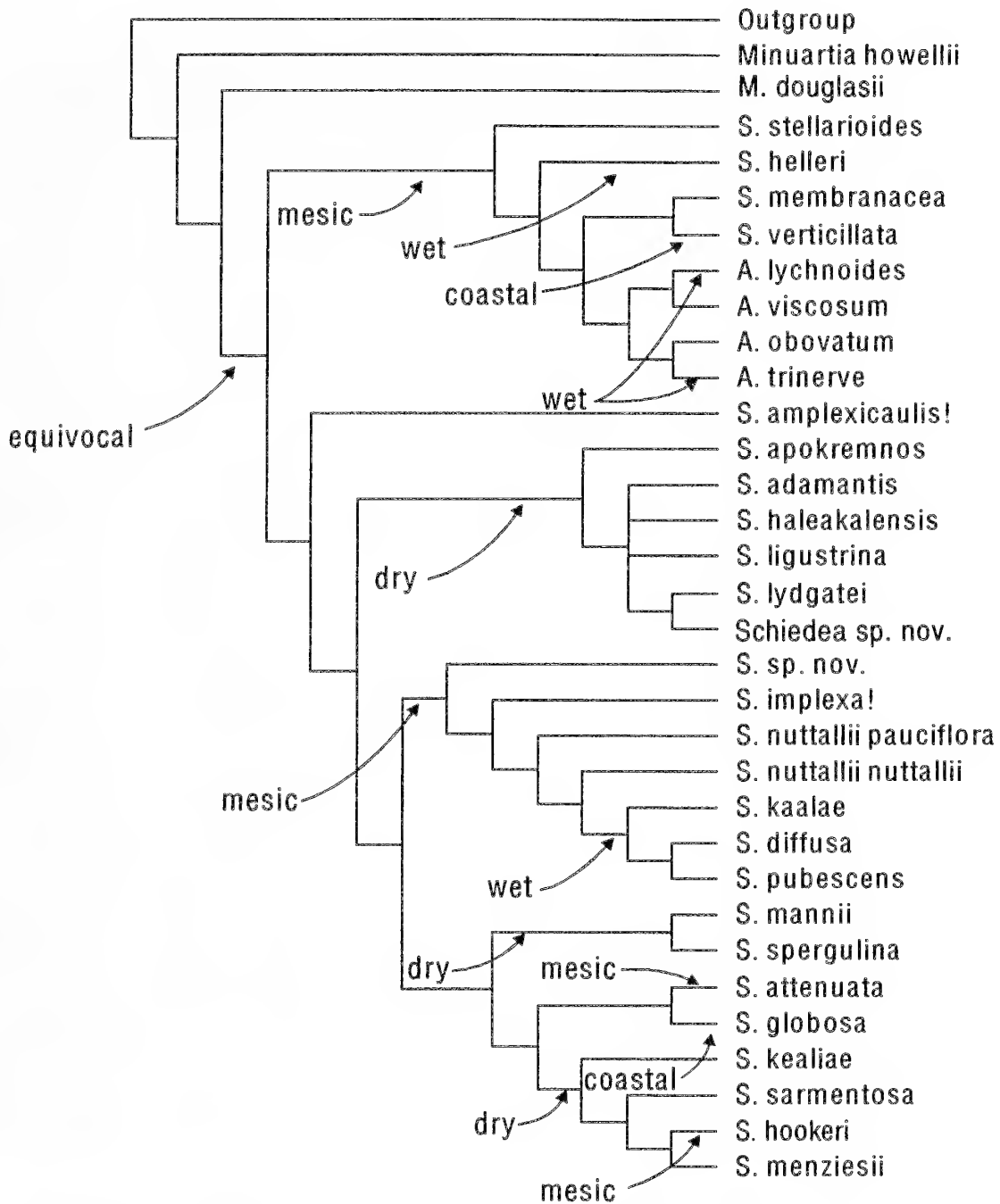


FIGURE 12.9. Hypothesis of habitat shifts in *Schiedea* and *Alsinidendron* mapped onto preferred tree using MacClade. The status of the common ancestor in the archipelago is equivocal and could have been in either a dry or a mesic habitat. Coastal habitats are dry.

of evolution in the clade comprising *S. hookeri*, *S. menziesii*, and *S. sarmentosa*. In one hypothesis (Figure 12.10A), a subdioecious ancestor gave rise to a hermaphroditic ancestor, followed by the evolution of gynodioecy in *S. sarmentosa*. In the other hypothesis (Figure 12.10B), a subdioecious ancestor gave rise to subdioecious, gynodioecious, and hermaphroditic derivatives. Using the DELTRAN option, however, there are five independent gains of dimorphism in the *S. globosa* clade in either topology. The results using MacClade were similar (Figure 12.10C),

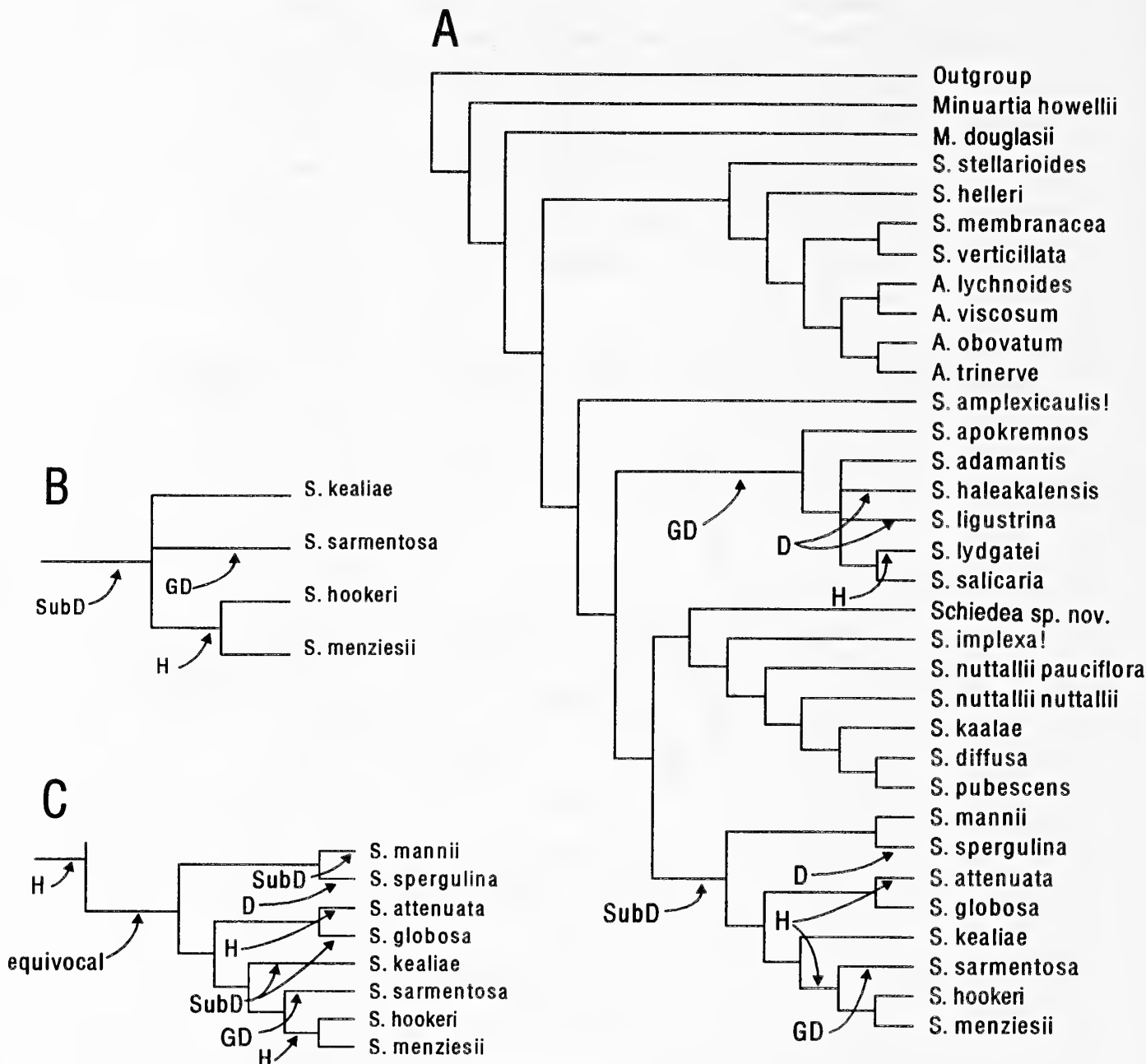


FIGURE 12.10. (A) Hypothesis of breeding system modifications in *Schiedea* and *Alsinidendron* mapped onto preferred tree using PAUP character reconstruction and the ACCTRAN option. An *exclamation mark* indicates an extinct species. Breeding system abbreviations are D, dioecious; GD, gynodioecious; H, hermaphroditic; SubD, subdioecious. Evolution of dimorphism is hypothesized to have occurred on three occasions; once in the *S. adamantis* clade and twice in the *S. globosa* clade. Note that reversals to hermaphroditism are hypothesized for both clades. (B) Alternative hypothesis of breeding system modifications in the *S. globosa* clade based on the other equally parsimonious topology. Evolution of both hermaphroditism and gynodioecy from a subdioecious ancestor is required. (C) Hypothesis of breeding system modifications in the *S. globosa* clade mapped onto preferred tree using MacClade. All branches leading to lineages within the *S. globosa* clade are equivocal, except for the common ancestor of *S. hookeri* and *S. menziesii*, which is hermaphroditic.

except that all interior nodes within the *S. globosa* clade were equivocal (either dimorphic or hermaphroditic), and the common ancestor of *S. hookeri* and *S. menziesii* was hermaphroditic.

DISCUSSION

Biogeographic Patterns

The known ages of the Hawaiian Islands coupled with our hypothesized phylogeny of the endemic Alsinoideae allow us to infer several biogeographic patterns. The phylogenetic hypotheses also clearly show how missing taxa, either because they are undiscovered or extinct, may obscure patterns of origin and colonization. The pattern exhibited within the basal *Schiedea membranacea* clade suggests that the original colonization to the archipelago for the endemic Hawaiian Alsinoideae occurred on islands that are now severely eroded and subsided. The *S. adamantis* and *S. nuttallii* clades originated on the oldest of the current main Hawaiian Islands (Kaua'i), and the *S. globosa* clade shows evidence of a more recent origin on O'ahu, although this result is equivocal using MacClade. Our phylogenetic analysis suggests that colonization then occurred from older to younger islands, with major diversification occurring on islands as they began their post-eruptive erosional stage. Inter-island colonizations (including back-colonizations) were often accompanied by speciation; two-thirds (14 of 22) of these colonizations have resulted in speciation.

Origin of the three terminal clades (the *Schiedea adamantis*, *S. nuttallii*, and *S. globosa* clades) on Kaua'i is suggested because of the basal species that occur on Kaua'i (see Figures 12.6 and 12.7). The origin of each clade appears to have been followed by parallel inter-island colonization to younger islands.

The analysis shows a different pattern within the *Schiedea membranacea* clade because its member species are largely restricted to Kaua'i (see Figures 12.6 and 12.7). A possible explanation is that extinction in this basal clade has obscured the process of colonization and diversification in this lineage. The *S. membranacea* lineage may have originated and diversified on an island older than Kaua'i and subsequently experienced significant extinction of all but a few species. An alternative hypothesis is that the pattern of diversification and colonization was different in the past, although there is little reason to believe that this would have occurred.

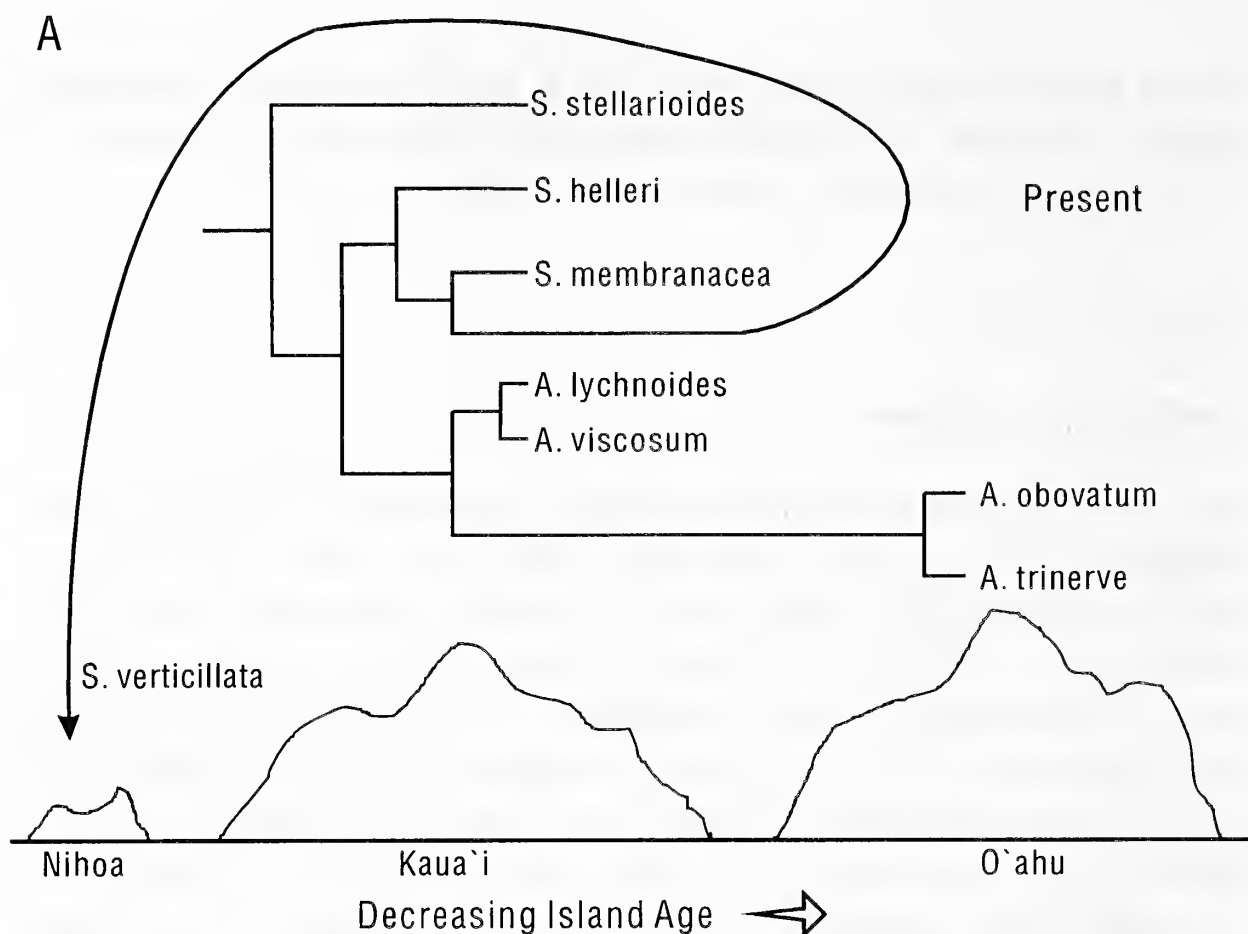


FIGURE 12.11. Comparison of two alternative interpretations of the biogeography of the *Schiedea membranacea* clade, which includes diverse species of *Schiedea* and the four species of *Alsinidendron*. (A) The biogeographic hypothesis directly indicated by our analyses for the *S. membranacea* clade. A back-colonization to Nihoa is indicated for *S. verticillata*. (B) Hypothetical pattern in which the pattern of diversification is modeled after a pattern similar to those currently observed for the clades on the current younger islands. *Dashed lines* indicate extinct lineages. (Continued on next page)

If Kaua'i was colonized by several elements of a diversified *Schiedea membranacea* clade, subsequent extinction has allowed disparate surviving species to be grouped together as a monophyletic clade of approximately the same size as the remaining three lineages in which there has been less extinction. To illustrate this, we contrasted the biogeographic hypothesis directly indicated by our analyses for the *S. membranacea* clade (Figure 12.11A) with a hypothetical pattern (Figure 12.11B) in which the pattern of diversification on older islands was similar to that currently observed for the clades on the current younger islands. The direct hypothesis indicates an origin on Kaua'i with a back-colonization to Nihoa for *S. verticillata* (Figure 12.11A), whereas in our hypothetical phylogeny, the clade originated on Necker Island, with subsequent further diversification on Nihoa and Necker (Figure 12.11B). The hypothet-

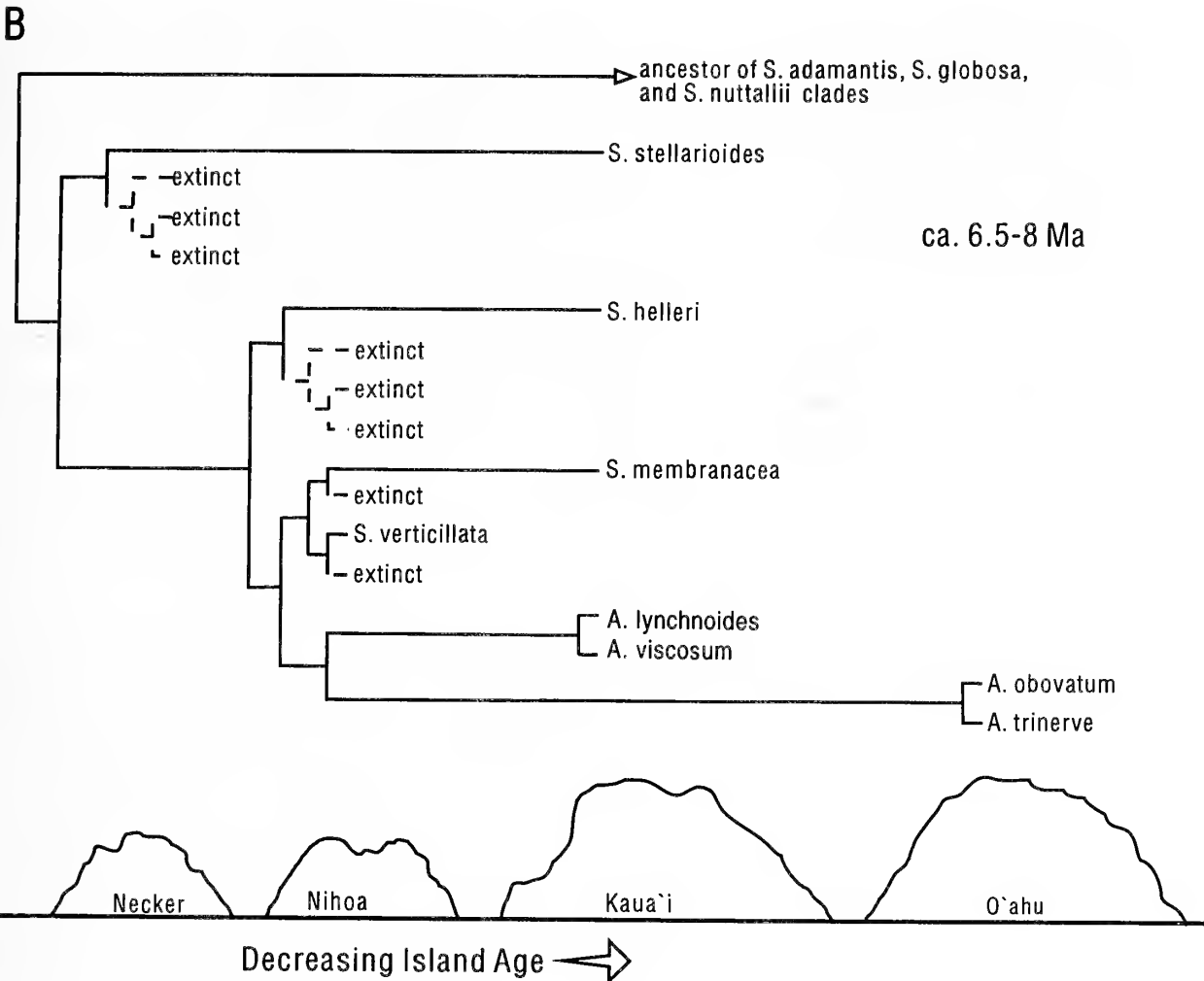


FIGURE 12.11. (Continued)

ical diversification of the *S. membranacea* lineage could have occurred between 6.5 and 8 million years ago (Ma), when these islands were considerably larger (see Carson and Clague, this volume, Chapter 2) and in the positions occupied by the current younger main Hawaiian Islands of Maui and Hawai'i. Erosion and subsidence of Necker and Nihoa over the next several million years would have led to the extinction of all but the now-relictual members of the *S. membranacea* clade that were able to colonize the young island of Kaua'i, and *S. verticillata* on Nihoa. If this scenario is true, the *S. membranacea* clade, after extinction of most of its members, would represent the remnants of an older radiation of which only two species (*Alsinidendron obovatum* and *A. trinerve*) have colonized beyond Kaua'i.

The cladistic analysis suggests that the genus *Schiedea* is paraphyletic through exclusion of the four species of *Alsinidendron*. In our analysis, nine synapomorphies delimit *Alsinidendron*, and there is no doubt that these species form a highly distinctive monophyletic group within this Hawaiian radiation. Evidence for the paraphyletic nature of

Schiedea comes from Kaua'i alone, where the clade with *Alsinidendron* forms a sister-taxon relationship to several Kaua'i species of *Schiedea*. If these basal Kaua'i and the Nihoa species in the *S. membranacea* clade (*S. helleri*, *S. membranacea*, *S. stellarioides*, and *S. verticillata*) (see Figures 12.6 and 12.7) were to go extinct, as they will (unless they colonize a younger island) when Nihoa and Kaua'i erode and subside into the ocean, then the remaining species of *Alsinidendron* on O'ahu would have a sister-taxon relationship to *Schiedea*. At this point, there would be no argument that *Alsinidendron* would be recognized at the generic level. Hawaiian taxa for which there is no current evidence for paraphyly would undoubtedly have been classified as paraphyletic if phylogenetic analysis could have included extinct species on islands that are now nearly submerged. The distribution of taxa on islands arranged in a linear chronology of increasing age makes it easy to visualize the process of the conversion of Hawaiian taxa from paraphyletic to nonparaphyletic status, although clearly the process is not unique to this type of archipelago. We favor retention of generic rank for *Alsinidendron* because submerging the genus into *Schiedea* ignores the processes of evolutionary diversification and extinction evident in the Hawaiian Islands, especially on those islands that formerly occurred to the northwest of Kaua'i, which are now eroded and nearly submerged.

Terminal, more highly derived species may be less likely to initiate new radiations. For example, *Alsinidendron obovatum* and *A. trinerve* on O'ahu are autogamous species (Weller et al., in press a) that may lack the genetic variability necessary to exploit new habitats or undergo significant morphological modifications (cf. Soulé, 1980). In contrast, the remaining clades have radiated on the younger islands from a more plesiomorphic ancestor (see Figure 12.5). Because radiations on the younger islands have presumably involved less extinction than those on older islands, these clades are also more morphologically cohesive.

A summary of the biogeography of the endemic Alsinoideae indicates that colonization appears to occur from older to younger islands, as shown in Figures 12.12 and 12.13. Twenty-two inter-island colonizations are shown. The phylogenetic analysis did not fully resolve biogeographic patterns of colonization. Therefore, we have assumed a Kaua'i origin for the *Schiedea globosa* clade because this reduces back-colonizations, and in virtually all unambiguous cases in the analysis, colonization has been from older to younger islands. An O'ahu origin is assumed for the ancestor of the polytomy in the *S. adamantis* clade as in the PAUP analysis. We have also assumed a Moloka'i origin for the common ancestor of

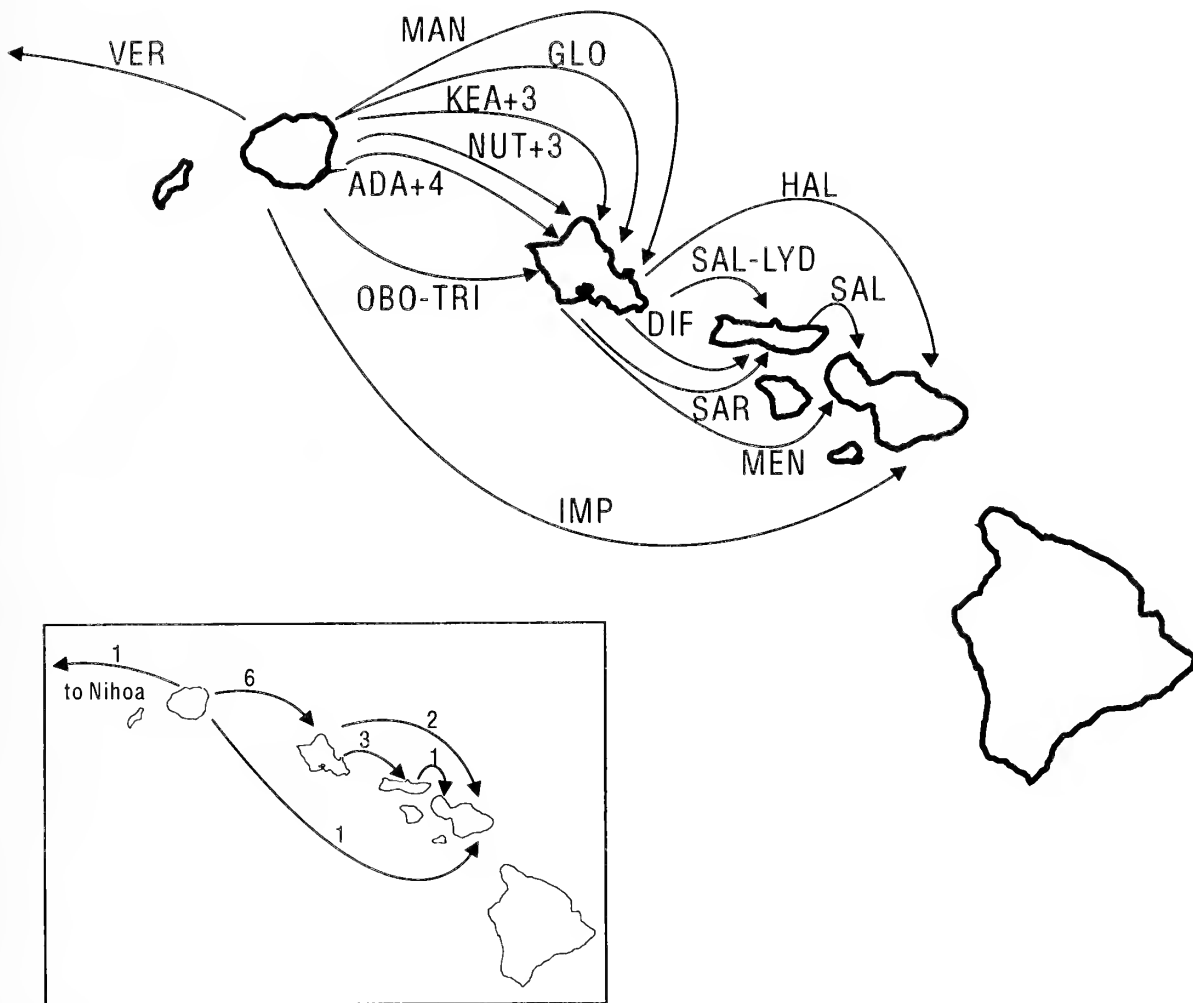


FIGURE 12.12. Summary of colonization events associated with speciation for current taxa and ancestors hypothesized for *Schiedea* and *Alsinidendron*. The first three letters of the specific epithets are used to indicate the species, except KEA+3, ancestor of *S. hookeri*, *S. kealiae*, *S. menziesii*, and *S. sarmentosa*; NUT+3, ancestor of *S. diffusa*, *S. kaalae*, *S. nuttallii* var. *nuttallii*, and *S. pubescens*; and ADA+4, ancestor of *S. adamantis*, *S. haleakalensis*, *S. ligustrina*, *S. lydgatei*, and *S. salicaria*. Ancestors of species pairs are indicated by a hyphenated acronym. Inter-island colonizations involving speciation are those indicated by the biogeographic analysis (using Figure 12.7 and assuming a Kaua'i origin for the *S. globosa* clade and an O'ahu origin for the ancestor of the polytomy in the *S. adamantis* clade). We have made three other assumptions in constructing the diagram: (1) a Moloka'i origin for the common ancestor of the *S. lydgatei*–*S. salicaria* pair, as discussed for Figure 12.6; (2) an O'ahu origin for *S. pubescens* and a Moloka'i origin for *S. diffusa*; and (3) and a West Maui origin for *S. menziesii*. The *inset* provides a summary of inter-island colonizations associated with speciation.



FIGURE 12.13. Possible sequence of inter-island colonizations for *Schiedea* and *Alsinidendron* without speciation implied by the biogeographic analysis. When more than one interpretation is possible, we have shown colonization to occur over the shortest distance. The pattern of colonization we prefer among several alternatives for *S. globosa* is a stepping-stone hypothesis. The first three letters of the specific epithets are used to indicate the species.

S. lydgatei and *S. salicaria* because this assumption involves a shorter colonization distance and follows the past land connection between O'ahu, Moloka'i, and Maui (see Carson and Clague, this volume, Chapter 2). The origins of species with multiple-island distributions are not resolved by our analysis, and we have made arbitrary assumptions for these. They include an O'ahu origin for *S. pubescens*, a Moloka'i origin for *S. diffusa*, and a West Maui origin for *S. menziesii*.

Patterns of origin and colonization must be interpreted in the light of the potentially strong influence of unknown extinct and undiscovered extant taxa. The back-colonization to Nihoa by *Schiedea verticillata* may represent an artifact resulting from significant extinction of a clade that occurred on older islands (cf. Figure 12.11B). This species is characterized by many specialized features and seems unlikely to have the Kaua'i ancestor implied in the analysis. The back-colonizations indicated by PAUP in the *S. globosa* clade also could be artifacts if there are extinct or undiscovered basal taxa in the *S. globosa* clade occurring on Kaua'i. This point is illustrated by the recent discovery of a new, undescribed basal species in the *S. nuttallii* clade that, when included in the analysis,

indicates clearly that this clade originated on Kaua'i. Until the discovery of this species, our analyses suggested that the *S. nuttallii* clade had originated on O'ahu, with the occurrence of *S. nuttallii* var. *pauciflora* on Kaua'i explained by a back-colonization.

Using MacClade's character reconstructions, the origin of the *Schiedea globosa* clade is uncertain, and thus it becomes unclear whether *S. spergulina* and *S. attenuata* represent back-colonizations. As discussed above, we tend to favor the interpretation of a Kaua'i or older island origin for all the clades.

Most inter-island colonizations also resulted in speciation (Figure 12.12); only eight inter-island colonizations did not involve speciation (Figure 12.13). Of the latter, five colonizations occurred within the Maui Nui complex. Colonization within the Maui Nui complex was presumably easier because these islands formed a single island during the Pleistocene. *Schiedea globosa* apparently colonized from Moloka'i to Maui or vice versa rather than with a second colonization from O'ahu. Colonization between Moloka'i and Maui seems more likely because these islands are closer to each other than to O'ahu and because allozyme data for *S. globosa* (Weller et al., in press a) show a closer relationship between the Maui and Moloka'i populations than either shows to the O'ahu populations.

Habitat Shifts

Character reconstruction using PAUP suggests that when the ancestor of *Schiedea* and *Alsinidendron* colonized the Hawaiian Islands it occurred in mesic habitats (see Figure 12.8). The members of the basal *S. membranacea* clade are still largely restricted to these habitats. A major shift from mesic to dry habitats occurred in the ancestor of the three terminal clades, followed by a reversal to mesic habitats at the base of the *S. nuttallii* clade. Species in this clade have apparently adapted to progressively wetter habitats, culminating in *S. diffusa*, where seeds germinate in situ on the plant, an adaption to extremely wet habitats. In addition to the invasion of dry habitats that occurred in the ancestor of the three terminal clades, a second switch to dry habitats has occurred for *S. verticillata*. Because this species may be the sole extant remnant of a much larger clade within the *S. membranacea* complex, there may have been a larger radiation of species into dry habitats in the basal lineage than suggested by the current distribution of species. Shifts from mesic to dry habitats may have occurred repeatedly throughout the evolutionary history of the endemic Hawaiian Alsinoideae.

Using MacClade, the number and timing of habitat shifts are less resolved (see Figure 12.9). In one alternative, the ancestor of the entire Hawaiian lineage colonized a dry habitat, followed by two independent shifts to mesic habitats in the *Schiedea nuttallii* and *S. membranacea* clades. In the other alternative, the original ancestor colonized a mesic habitat, with four separate ecological shifts to dry habitats. *Minuartia douglasii* and *M. howellii*, outgroup species for the endemic Hawaiian Alsinoideae, occur in dry habitats, providing some support for the former hypothesis. This outgroup comparison is not particularly helpful, however, because the extra-Hawaiian habitats of these two annual *Minuartia* species, although dry, are not comparable in other respects to the habitats in the Hawaiian Islands.

Evolution of Breeding Systems

Character reconstructions using PAUP with the ACCTRAN and DELTRAN options indicate that dimorphism has evolved independently in the *Schiedea adamantis* and *S. globosa* lineages (see Figure 12.10A). Gynodioecy is basal in the *S. adamantis* clade, with subsequent evolution of dioecy in *S. haleakalensis* and *S. ligustrina*. Hermaphroditism in *S. lydgatei* apparently represents a reversal from dimorphism, as this species is well nested within a clade containing only dimorphic species. *Schiedea salicaria*, the sister taxon of *S. lydgatei*, has a gynodioecious breeding system with only 12% females in the populations investigated (Weller et al., 1990; A. K. Sakai and S. G. Weller, unpubl.), suggesting that a reversal to hermaphroditism from gynodioecy in the common ancestor would be relatively easy (F. R. Ganders, unpubl.).

Subdioecy is basal in the *Schiedea globosa* lineage using character reconstruction with ACCTRAN. Two alternative phylogenies in this lineage yield different suggestions for the evolution of dimorphism, and both involve the reversion to hermaphroditism from subdioecy. In one tree (see Figure 12.10A), hermaphroditism evolves from subdioecy, and gynodioecy subsequently evolves in *S. sarmentosa*. The extra instance of the evolution of dimorphism in this tree seems reasonable, as this breeding system is often predicted to be the first stage in the evolution of full dioecy (Lloyd, 1975; Charlesworth and Charlesworth, 1978). In the alternative tree (see Figure 12.10B), gynodioecy and hermaphroditism evolve from a subdioecious ancestor.

Use of DELTRAN for character reconstruction results in five independent transitions to dimorphism in terminal taxa of the *Schiedea globosa*

clade, in contrast to the reversal from dimorphism to hermaphroditism resulting with ACCTRAN. That such reversals can occur is suggested unequivocally for the *S. adamantis* clade, although the reversal in the *S. adamantis* clade involves a change from gynodioecy to hermaphroditism rather than a change from subdioecy to hermaphroditism. If such reversals are unlikely, character reconstructions using ACCTRAN may provide a less realistic view of breeding system evolution in the *S. globosa* clade than reconstructions using DELTRAN. Because character reconstructions using MacClade were equivocal for the *S. globosa* clade, dimorphism may have independently evolved only once or as many as five times (see Figure 12.10C) in the *S. globosa* clade.

Earlier work (Weller et al., 1990) suggested that hermaphroditic species were more likely to undergo inter-island colonization than dimorphic species, a suggestion consistent with Baker's (1967) law applied within the Hawaiian Islands. The subsequent discovery of two additional single-island endemic hermaphroditic species (*Schiedea attenuata* and *Schiedea* sp. nov.) now indicates that breeding systems in the endemic Hawaiian Alsinoideae have little effect on the likelihood of inter-island colonization. Moreover, it originally appeared that dimorphic species were more likely to be found on the older islands of Kaua'i and O'ahu (Weller et al., 1990). With the discovery of gynodioecy in the recently resurrected *S. sarmentosa* on Moloka'i and dioecy in *S. haleakalensis* on East Maui, it is now clear that dimorphism is as likely to occur on the younger as the older Hawaiian Islands.

Patterns of Speciation

In addition to the original transoceanic colonization of the Hawaiian Islands, the phylogenetic analysis implies that at least 56 speciation events have occurred in the radiation of the endemic Hawaiian Alsinoideae. This number includes interior and terminal nodes of a phylogeny constructed from extant taxa and assumes that the ancestral species go extinct at each branching point. Of these, 14 (25%) appear to have been inter-island colonizations and 42 appear to have occurred within islands. Using only the extant taxa, 9 (30%) of 30 taxa evolved concomitant with inter-island colonization (cf. Figures 12.12 and 12.13), suggesting that patterns of speciation during colonization at interior nodes of the cladogram are consistent with those occurring at the endpoints. Thus, biogeographic analysis indicates that most speciation in the endemic Hawaiian Alsinoideae has been intra-island. Unfortunately, it is impossible to deter-

mine if speciation is disproportionately associated with intra-island rather than inter-island colonization events. Although we can identify the number of successful inter-island colonization events with and without speciation and we can identify the successful intra-island colonizations with speciation, it is extremely difficult to know the number of independent colonizations within an island that did not result in speciation but simply led to new populations of the same species.

Inter-island speciation may be overestimated because of past land connections between most of the current islands (see Carson and Clague, this volume, Chapter 2). For example, two very similar sister taxa, *Schiedea lydgatei* and *S. salicaria*, occur on eastern Moloka'i and West Maui, islands that were connected in the past. Speciation could have occurred as a consequence of the recent isolation and separation of the volcanoes as separate islands formed with increasing post-Pleistocene sea levels.

Other evidence for this phenomenon is found for species with multiple-island distributions. Three of the five species occurring on more than one island have distributions within the Maui Nui complex (*Schiedea diffusa*, *S. menziesii*, and *S. pubescens*). All these may have spread throughout Maui Nui when it was a single island. In contrast, the distribution of *S. globosa* on dry coastal cliffs of O'ahu, Moloka'i, and Maui may be the result of inter-island rafting, as fragments of this species have been observed floating below sea cliffs (W. L. Wagner, unpubl.).

If the hypothesized collapse of the *Schiedea membranacea* clade actually occurred, this would result in a failure to detect colonization from older, now-eroded and nearly submerged islands. Consequently, the number of intra-island speciation events would be overestimated. As discussed earlier, some species of the *S. membranacea* lineage are likely to represent the remnants of clades in which most species are extinct, and speciation events may well have been inter-island but undetected. The morphological similarity of *Alsinidendron lychnoides* and *A. viscosum*, however, suggests that these species probably share a recent origin on Kaua'i. They occur in different habitats, indicating that ecological differentiation has played a significant role in speciation. Similarly, *A. obovatum* and *A. trinerve* appear closely related but occur in different habitats in the Wai'anae Mountains on O'ahu.

Within the *Schiedea adamantis* clade, the origins of *S. adamantis* and *S. ligustrina* represent intra-island speciation events that occurred in similar habitats but involved colonization of different volcanoes. *Schiedea ligustrina* is scattered throughout the Wai'anae Mountains of

western O‘ahu, whereas *S. adamantis* is now restricted to a single population consisting of several hundred individuals on Diamond Head Crater of southeastern O‘ahu. *Schiedea adamantis* may have been more widespread in the leeward Ko‘olau Mountains before the expansion of Honolulu, although the very restricted allozyme variation found in this population suggests that the species may have originated through a recent founder event and never occurred in more than a single population (Weller et al., in press a). In either case, there is no indication that *S. adamantis* ever occurred in or near the Wai‘anae Mountains. The remaining intra-island speciation event in the *S. adamantis* clade involves *S. apokremnos*, which our phylogeny suggests evolved from an ancestor occurring in dry habitats on Kaua‘i.

Considering intra-island speciation events in the *Schiedea globosa* clade, *S. hookeri* and *S. kealiae* originated in the Wai‘anae Mountains but now occupy different habitats (see Table 12.1) and occur in slightly different geographic regions of the Wai‘anae Mountains. On O‘ahu, *S. globosa* occurs at the southeastern tip of the island, well removed from the center of diversity of the clade in the Wai‘anae Mountains, and is restricted to dry coastal cliffs. Thus, if the clade originated on O‘ahu, *S. globosa* had an intra-island allopatric origin as well as a concomitant shift in habitat. If the clade arose on Kaua‘i, then *S. globosa* had an inter-island origin. *Schiedea mannii* represents an intra-island speciation event (unless the clade originated on Kaua‘i), but as in the case of *S. apokremnos*, *S. mannii* is hypothesized to have evolved from an ancestor occurring in dry habitats.

Within the *Schiedea nuttallii* clade, several intra-island speciation events occurred on Kaua‘i and in the Wai‘anae Mountains. *Schiedea nuttallii* var. *pauciflora* and the new species represent intra-island speciation events on Kaua‘i. No habitat shifts are indicated. Present distributions suggest allopatric origins for both species, although habitat and distributional data are fragmentary. On O‘ahu, *S. kaalae* overlaps in geographic distribution with *S. nuttallii* var. *nuttallii* but occurs in wetter habitats. A third species, *S. pubescens*, occurs in wet habitats but at generally higher elevations. *Schiedea diffusa*, which probably originated on Moloka‘i, presumably represents colonization associated with speciation and prefers far wetter habitats than any other species in the *S. nuttallii* clade.

Intra- and inter-island speciation events for the 30 extant taxa of the endemic Alsinoideae are summarized in Figure 12.14. This figure represents a subset of the inter-island colonizations present in Figure 12.12. More than two-thirds of these represent intra-island speciation events, suggesting that inter-island colonization is not necessary for speciation in

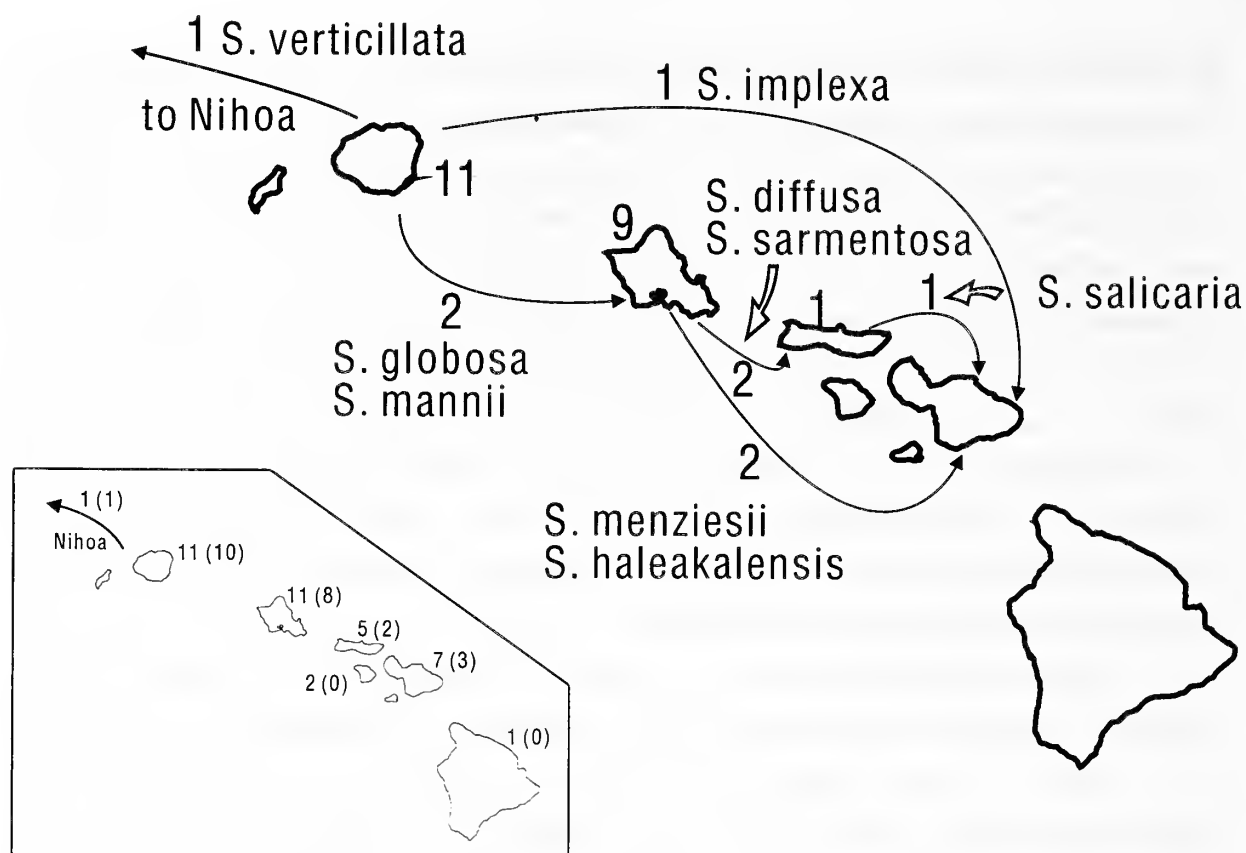


FIGURE 12.14. Summary of inter-island and intra-island speciation events, based on Figures 12.12 and 12.13 (excluding interior node ancestor colonizations; see Figures 12.6 and 12.7). The numbers adjacent to Kaua'i, O'ahu, and Molokai indicate the numbers of intra-island speciation events on those islands. The *inset* shows the total number of species occurring on each island, and the number of endemic taxa is given in parentheses.

this group. Many of these intra-island speciation events, however, are associated with ecological shifts. In contrast, only three of the eight cases of inter-island colonization associated with speciation seem to be associated with habitat shifts. *Schiedea haleakalensis*, found in dry subalpine habitat, represents the most striking case of a habitat shift associated with colonization. *Schiedea verticillata* and *S. attenuata* may be cases of habitat shifts associated with colonization, but their apparent sister-taxon relationships may be artifacts (see discussion above). The remaining five cases of inter-island speciation with colonization events probably occurred without habitat shifts, although in the MacClade analysis, two of the five cases are equivocal.

SUMMARY

Diversification in the monophyletic lineage that comprises the endemic Alsinoideae, perhaps from a North American ancestor related to

Minuartia, has resulted in remarkable shifts in morphology, habitat, and breeding system. This diversification has involved the evolution of four main clades, with *Alsinidendron* nested within the basal clade. These changes have occurred primarily as colonization has proceeded from older to younger islands. Phylogenetic evidence suggests that the endemic Alsinoideae originally diversified on islands that have now largely eroded and subsided beneath the ocean. Extinction of species in basal lineages results in compression of older lineages into a single diverse basal clade containing species that have accumulated many specialized characters. In the endemic Alsinoideae, diversification apparently has occurred during the first 1 to 2 million years after an island emerges from the ocean. As these islands age, the occasional colonization to a newly formed island by unspecialized species results in the diversification of new lineages. Despite the significance of colonization, more than two-thirds of the speciation events have taken place without inter-island colonization. These intra-island speciation events usually are associated with geographic or ecological shifts. When speciation has been associated with inter-island colonization, there is less evidence for significant changes in habitat.

Main trends in the endemic Alsinoideae include the invasion of dry habitats and shifts on several occasions from hermaphroditic to dimorphic breeding systems. Phylogenetic information, however, provides clear evidence that in at least one case (*Schiedea lydgatei*) a reversal from dimorphism to hermaphroditism has occurred. A second reversal is indicated, but results are less conclusive. This study provides insights into the overall patterns of morphological diversity in *Schiedea* and *Alsinidendron* and aids in the interpretation of evolutionary events associated with breeding system modification.

ACKNOWLEDGMENTS

We thank the Scholarly Studies Program of the Smithsonian Institution, the National Geographic Society, and the National Science Foundation (BSR 88-17616, BSR 89-18366, DEB 92-07724) for support of this research. We appreciate support from the National Tropical Botanical Garden, Lawa'i; in particular, the Hawaii Plant Conservation Center provided seeds of *Alsinidendron lychnoides*, *A. obovatum*, *A. viscosum*, *Schiedea apokremnos*, *S. attenuata*, *S. helleri*, *S. membranacea*, *S. pubescens*, *S. spergulina*, and *S. stellarioides*. The resources of the Bishop Museum have been invaluable. We appreciate the assistance in

collection of morphological data from Mike Sisson. We thank Elizabeth Harris, Robynn Shannon, and Alice Tangerini for adding clarity and dimension to this chapter through preparation of the scanning electron microscopy study presented in Figure 12.2, Figures 12.3 to 12.14, and the habit drawings in Figure 12.1, respectively. We thank V. A. Funk for discussion of ideas and Tim Lowrey and Richard Rabeler for comments on the manuscript. Without the help of Joan Aidem, Melany Chapin, Tom Egeland, Bruce Eilerts, Tim Flynn, Norm Glenn, Bill Haus, Robert Hobdy, Guy Hughes, Joel Lau, David Lorence, John Obata, Art Medeiros, Steve Perlman, Lyman Perry, Diane Ragone, Wayne Takeuchi, Patti Welton, and Ken Wood, this research would not have been possible.

APPENDIX 12.1. Character List for *Schiedea* and *Alsinidendron*

1. Presence of woody tissue: 0 = herbaceous; 1 = suffrutescent sprawler; 2 = woody.
2. Stems persistent or deciduous: 0 = stems persistent; 1 = stems deciduous above ground.
3. Habit: 0 = stems upright; 1 = stems sprawling; 2 = vine.
4. Roots: 0 = fibrous roots; 1 = swollen, fleshy root.
5. Stem succulence: 0 = stems slender; 1 = stems thick and somewhat fleshy.
6. Leaf shape: 0 = leaves broadest at or below middle; 1 = leaves broadest above middle; 2 = leaves linear or oblong.
7. Leaf texture: 0 = leaves membranous; 1 = leaves coriaceous; 2 = leaves softly membranous.
8. Leaf size: 0 = leaf of intermediate area; 1 = leaf area large.
9. Leaf succulence: 0 = leaves not succulent; 1 = leaves succulent.
10. Leaf symmetry: 0 = leaves symmetric; 1 = leaves slightly asymmetric; 2 = leaves falcate; 3 = midvein of leaf conspicuously off-center.
11. Leaf apex: 0 = acute or acuminate; 1 = long-attenuate.
12. Reduction in leaf venation: 0 = leaves 3-nerved or more; 1 = 1-nerved.
13. Increase in leaf venation: 0 = 1- or 3-nerved; 1 = 5-nerved; 2 = 7-nerved or more.
14. Outer leaf veins arc: 0 = outer primary veins forming a broadly rounded arch; 1 = outer primary veins widely looping along margin.
15. Pubescence of leaf margin: 0 = no pubescence; 1 = thin hairs; 2 = hooked hairs.
16. Leaf margin: 0 = margin entire; 1 = minute irregular teeth; 2 = minute serrations, especially distal part; 3 = serrate.
17. Leaf pubescence: 0 = hairs glandular, clear; 1 = glabrous; 2 = nonglandular hairs, clear; 3 = hairs with purple pigment; 4 = hairs on adaxial midrib and leaf base margin.

18. Leaf surface: 0 = not glaucous; 1 = leaves slightly glaucous.
19. Lateral inflorescence condensation (breeding system): 0 = inflorescence open, paniculate cymes; 1 = lateral inflorescence branches shortened, main axis elongate.
20. Inflorescence main axis condensation (breeding system): 0 = inflorescence open, paniculate cymes; 1 = main axis somewhat vertically condensed; 2 = main axis highly vertically condensed; 3 = inflorescence globose, due to nearly complete suppression of main axis.
21. Suppression of inflorescence main axis: 0 = main axis present and developed; 1 = main axis suppressed, represented by a single terminal flower; 2 = main axis suppressed, laterals moderately suppressed.
22. Pedicel presentation: 0 = strongly ascending, flowers upright; 1 = recurved, flowers pendent.
23. Inflorescence presentation: 0 = inflorescences upright; 1 = inflorescences pendent.
24. Inflorescence pubescence: 0 = glandular pubescence, hairs of medium length; 1 = glabrous; 2 = short glandular pubescence; 3 = long glandular pubescence; 4 = nonglandular pubescence; 5 = glandular purple pubescence; 6 = nonglandular purple pubescence.
25. Sepal width: 0 = <3 mm; 1 = >5 mm.
26. Calyx configuration: 0 = erect or reflexed; 1 = calyx campanulate; 2 = calyx closed or nearly so at anthesis.
27. Sepal orientation: 0 = spreading to slightly reflexed; 1 = ascending; 2 = strongly reflexed.
28. Sepal texture: 0 = membranous, green; 1 = membranous, white, remaining papery as fruit matures; 2 = fleshy, white or green, becoming dark purple and juicy as fruit matures.
29. Sepal apex: 0 = obtuse to acute; 1 = attenuate to caudate.
30. Sepal symmetry: 0 = symmetric; 1 = irregular.
31. Sepal margin pubescence: 0 = glabrous; 1 = ciliate.
32. Nectary type: 0 = small mound; 1 = nectary with well-developed hypodermic syringelike shaft, extending beyond the \pm bulbous basal nectariferous portion; 2 = nectary with well-developed flap, extending beyond the bulbous nectariferous portion, the flaps not connate at base; 3 = similar to 2, but flaps connate at base or into a cup around ovary.
33. Nectary curvature (*Schiedea* only): 0 = straight, nectar deposited in a drop at apex; 1 = recurved, nectar deposited on concave surface of sepal.
34. Nectar color: 0 = clear; 1 = black, when large amount accumulates.
35. Ratio, staminal filament/sepal length (breeding system): 0 = <1; 1 = 1–1.9; 2 = ≥ 2.0 .
36. Anther color: 0 = yellow; 1 = coral.
37. Pollen color: 0 = yellow; 1 = gray.
38. Style number: 0 = 3–4; 1 = 4–6; 2 = 5–11.

39. Ovule number: 0 = <100; 1 = >100.
40. Seed retention: 0 = seeds dispersed through open valves; 1 = seeds retained in capsule, gradual rotting releases seeds.
41. Seed margin: 0 = cells along seed margin not elongate; 1 = cells along margin moderately to strongly elongated into papillae.
42. Cell margin shape on seed surface: 0 = cell lobes appear rounded to convex because cells convex; 1 = cell lobes appear acute because cells flat.
43. Breeding system (excluded): 0 = hermaphroditic; 1 = gynodioecious; 2 = subdioecious; 3 = dioecious.
44. Habitat (excluded): 0 = California chaparral and woodland; 1 = mesic forest; 2 = dry slopes and cliffs; 3 = coastal; 4 = wet forest.
45. Island distribution (excluded): 0 = California; 1 = Kaua'i; 2 = O'ahu; 3 = Moloka'i; 4 = West Maui; 5 = East Maui; 6 = Lana'i; 7 = Hawai'i; 8 = Nihoa.

APPENDIX 12.2. Data Matrix of Morphological Character States of *Schiedea* and *Alsinidendron*

The characters and character states are defined in Appendix 12.1. Missing data are indicated by question marks. Other symbols for polymorphic characters or multiple-island distributions are a = 0, 1; b = 1, 2; c = 1, 4; d = 2, 3, 4, 5; e = 3, 5, 7; f = 4, 6; g = 2, 3, 4, 5, 6. Information on characters 43 to 45 is also given in Table 12.1.

[illegible]

13

Historical Biogeography and Ecology of the Hawaiian Silversword Alliance (Asteraceae)

New Molecular Phylogenetic Perspectives

BRUCE G. BALDWIN AND
ROBERT H. ROBICHAUX

The silversword alliance comprises 28 endemic Hawaiian Islands species of the sunflower family (Asteraceae) that are circumscribed within the genera *Argyroxiphium*, *Dubautia*, and *Wilkesia* (Carr, 1985). This assemblage is best known from the five species of *Argyroxiphium* (Table 13.1), the silverswords and greenswords, which are among the most visually spectacular plants in the indigenous Hawaiian flora. *Argyroxiphium* species are characterized by a basal or slightly elevated rosette of green or silvery haired, swordlike leaves from which emerges a terminal capitulescence of up to 600 large rayed heads (Carr, 1985). This massive flowering stalk can reach up to 2 m tall in the well-known silversword *A. sandwicense* (Figure 13.1), a frequently monocarpic plant of dry alpine habitats on Haleakala, Maui, and Mauna Kea, Hawai'i. The three other extant species of *Argyroxiphium* are also found at high elevations on Maui and Hawai'i (Figure 13.2) but are bog and wet forest inhabitants that may branch from the base to produce multiple leaf rosettes.

The silverswords and greenswords represent less than 20% of the species diversity in the silversword alliance; 23 additional species are currently recognized in *Dubautia* and *Wilkesia* (Carr, 1985) (Table 13.1). The 21 species of *Dubautia* are distributed across six of the eight main islands of the Hawaiian archipelago (Kaua'i, O'ahu, Moloka'i, Lana'i, Maui, Hawai'i) (Figure 13.2), with all but four species being single-island endemics. Both species of *Wilkesia* are

TABLE 13.1. Collections, Geographic Distributions, and Habitats of 36 Hawaiian Silversword Alliance Populations, 5 California Floristic Province Tarweeds, and 2 Outgroup Species Examined for Variation in ITS Nucleotide Sequences

| Collection ^a | Distribution ^b | Habitat |
|--|-----------------------------|---------|
| Outgroups | | |
| <i>Arnica mollis</i> Hook., BGB 680, Sierra Nevada, California | Western North America | Wet |
| <i>Hulsea algida</i> A. Gray, BGB 678, Sierra Nevada, California | Western North America | Dry |
| California Floristic Province Madiinae | | |
| <i>Adenothamnus validus</i> (Brandege) Keck, MSW 86–99, Punta Banda, Baja California, Mexico | California FP of BC, Mexico | Dry |
| <i>Madia bolanderi</i> (A. Gray) A. Gray, BGB 509, Rubicon Creek, Lake Tahoe vicinity, Sierra Nevada, California | California FP | Wet |
| <i>Raillardiopsis</i> | | |
| <i>R. muirii</i> (A. Gray) Rydb., BGB 618, Ventana Double Cone, Santa Lucia Range, California | California FP | Dry |
| <i>R. scabrida</i> (Eastw.) Rydb., BGB 676, Hull Mountain, North Inner Coast Range, California | California FP | Dry |
| <i>Raillardella pringlei</i> E. Greene, BGB 608, Toad Lake, Scott Mountains, California | California FP | Wet |
| Hawaiian Islands Madiinae (Silversword Alliance) | | |
| <i>Argyroxiphium</i> | | |
| <i>A. caliginis</i> C. Forbes, BGB 680, Pu‘u Kukui, West Maui | Maui Nui | Wet |
| <i>A. grayanum</i> (Hillebr.) Degener, BGB 661, Pu‘u Kukui, West Maui | Maui Nui | Wet |
| <i>A. grayanum</i> (Hillebr.) Degener, AM s. n., Haleakala, East Maui | Maui Nui | Wet |
| <i>A. kauense</i> (Rock & M. Neal) Degener & I. Degener, BGB 773 (DUKE), saddle between Mauna Loa and Mauna Kea, Hawai‘i | Hawai‘i | Wet |
| <i>A. sandwicense</i> DC. subsp. <i>macrocephalum</i> (A. Gray) Meyrat, GDC 1239, Haleakala, East Maui | Maui Nui | Dry |
| <i>A. sandwicense</i> DC. subsp. <i>sandwicense</i> , BGB 657, Mauna Kea, Hawai‘i | Hawai‘i | Dry |
| <i>Dubautia</i> sect. <i>Dubautia</i> | | |
| <i>D. imbricata</i> H. St. John & G. Carr subsp. <i>imbricata</i> , BGB 667, Wahiawa Mountains, Kaua‘i | Kaua‘i | Wet |
| <i>D. knudsenii</i> Hillebr. subsp. <i>filiformis</i> G. Carr, GDC 1234, Makaleha Mountain, Kaua‘i | Kaua‘i | Wet |
| <i>D. knudsenii</i> Hillebr. subsp. <i>knudsenii</i> , GDC 1047, Koke‘e Park, Kaua‘i | Kaua‘i | Wet |
| <i>D. knudsenii</i> Hillebr. subsp. <i>nagatae</i> (H. St. John) G. Carr, GDC 1322, Alaka‘i Swamp, Kaua‘i | Kaua‘i | Wet |

TABLE 13.1. (Continued)

| Collection ^a | Distribution ^b | Habitat |
|--|---------------------------|---------|
| <i>Dubautia</i> sect. <i>Dubautia</i> (cont.) | | |
| <i>D. laevigata</i> A. Gray, BGB 671, Trailhead, Koke'e Park, Kaua'i | Kaua'i | Wet |
| <i>D. laevigata</i> A. Gray, BGB 777 (DUKE), Kalalau Lookout vicinity, Koke'e Park, Kaua'i | Kaua'i | Wet |
| <i>D. laxa</i> Hook. & Arnott subsp. <i>hirsuta</i> (Hillebr.) G. Carr, GDC 833, Mt. Ka'ala, Wai'anae Range, O'ahu | Kaua'i, O'ahu, Maui Nui | Wet |
| <i>D. laxa</i> Hook. & Arnott subsp. <i>laxa</i> , BGB 662, Pu'u Kukui, West Maui | O'ahu, Maui Nui | Wet |
| <i>D. microcephala</i> Skotts., GDC 1044, Kahuama'a Flat, Koke'e Park, Kaua'i | Kaua'i | Wet |
| <i>D. paleata</i> A. Gray, GDC 1375, Alaka'i Swamp, Kaua'i | Kaua'i | Wet |
| <i>D. pauciflora</i> H. St. John & G. Carr, BGB 668, Wahiawa Mountains, Kaua'i | Kaua'i | Wet |
| <i>D. plantaginea</i> Gaud. "Blue Hole," BGB 776 (DUKE), Blue Hole, Kaua'i | Kaua'i | Wet |
| <i>D. plantaginea</i> Gaud. subsp. <i>humilis</i> G. Carr, GDC 1183, Black Gorge, West Maui | Maui Nui | Wet |
| <i>D. plantaginea</i> Gaud. subsp. <i>plantaginea</i> , GDC 1180, Ko'olau Range, O'ahu | O'ahu, Maui Nui, Hawai'i | Wet |
| <i>D. raillardii</i> Hillebr., BGB 670, Wahiawa Bog border, Kaua'i | Kaua'i | Wet |
| <i>Dubautia</i> sect. <i>Raillardia</i> | | |
| <i>D. arborea</i> (A. Gray) Keck, BGB 527, Mauna Kea, Hawai'i | Hawai'i | Dry |
| <i>D. ciliolata</i> (DC.) Keck subsp. <i>ciliolata</i> , BGB 529, Kilauea, Hawai'i | Hawai'i | Dry |
| <i>D. ciliolata</i> (DC.) Keck subsp. <i>glutinosa</i> G. Carr, BGB 659, Mauna Kea, Hawai'i | Hawai'i | Dry |
| <i>D. herbstobatae</i> G. Carr, GDC 1244, 'Ohikilolo Ridge, Wai'anae Range, O'ahu | O'ahu | Dry |
| <i>D. linearis</i> (Gaud.) Keck subsp. <i>hillebrandii</i> (H. Mann) G. Carr, BGB 531, Pohakuloa Military Reservation, Hawai'i | Hawai'i | Dry |
| <i>D. linearis</i> (Gaud.) Keck subsp. <i>linearis</i> , BGB 516, E. of 'Ulupalakua, East Maui | Maui Nui | Dry |
| <i>D. menziesii</i> (A. Gray) Keck, BGB 522, Haleakala, East Maui | Maui Nui | Dry |
| <i>D. platyphylla</i> (A. Gray) Keck, BGB 524, Haleakala, East Maui | Maui Nui | Dry |
| <i>D. reticulata</i> (Sherff) Keck, BGB 664, Ko'olau Gap, East Maui | Maui Nui | Wet |

(Continued)

TABLE 13.1. (Continued)

| Collection ^a | Distribution ^b | Habitat |
|--|---------------------------|------------------|
| <i>Dubautia</i> sect. <i>Railliardia</i> (cont.) | | |
| <i>D. scabra</i> (DC.) Keck subsp. <i>leiophylla</i> (A. Gray) G. Carr, BGB 778 (DUKE), Olinda Flume, East Maui | Maui Nui | Wet |
| <i>D. scabra</i> (DC.) Keck subsp. <i>scabra</i> , BGB 530, Kilauea, Hawai'i | Hawai'i | Wet ^c |
| <i>D. sherffiana</i> Fosb., BGB 515, Kamaile'unu Ridge, Wai'anae Range, O'ahu | O'ahu | Wet |
| <i>Dubautia</i> sect. <i>Venoso-reticulatae</i> | | |
| <i>D. latifolia</i> (A. Gray) Keck, BGB 675, Makaha Ridge, Koke'e Park, Kaua'i | Kaua'i | Wet |
| <i>Wilkesia</i> | | |
| <i>W. gymnoxiphium</i> A. Gray, Char 76.022, Waimea Canyon rim, Kaua'i | Kaua'i | Dry |
| <i>W. hobdyi</i> H. St. John, GDC 1150, Polihale Ridge, Kaua'i | Kaua'i | Dry |

^aCollections are identified as follows: BGB, B. G. Baldwin et al.; GDC, G. D. Carr; AM, A. Medeiros; MSW, M. S. Witter. Except where otherwise stated, BGB, AM, and MSW vouchers are at University of California, Davis (DAV). GDC and Char vouchers are at University of Hawai'i (HAW). Accessions not examined in previous cpDNA studies (Baldwin, 1989; Baldwin et al., 1990, 1991) include *Argyroxiphium kauense* (BGB 773), *Dubautia laevigata* (BGB 777), *D. plantaginea* "Blue Hole" (BGB 776), and *D. scabra* subsp. *leiophylla* (BGB 778). Three species were not sampled: *A. virescens* Hillebr., *D. dolosa* (Degener & Sherff) G. Carr, and *D. waialealae* Rock.

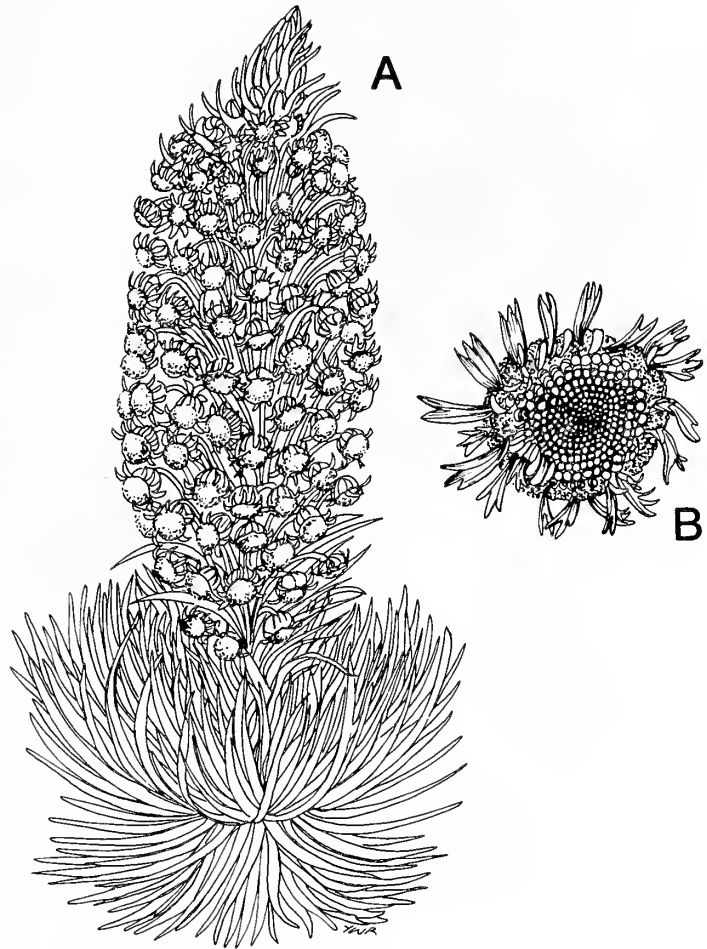
^bCalifornia FP, California Floristic Province (Howell, 1957; Raven and Axelrod, 1978). BC, Baja California. In the Maui Nui complex the silversword alliance species occur on Moloka'i, Maui, and Lana'i. For Hawaiian Islands Madiinae, geographic distributions are primarily from Carr (1985).

^cIn addition to growing in wet forests, *Dubautia scabra* subsp. *scabra* colonizes young lava flows in areas with relatively low annual rainfall. Although the flows have a dry appearance, the plants growing on them have access to abundant water supplies (Robichaux, 1984).

confined to dry western slopes on the oldest high island, Kaua'i. Unlike *Argyroxiphium*, all species of *Dubautia* and *Wilkesia* possess discoid capitula (i.e., lack ray flowers).

Together, *Wilkesia* and *Dubautia* encompass a tremendous range of growth forms, including rosette plants (Figure 13.3), trees, shrubs (Figure 13.4A and B), subshrubs (Figure 13.4C), cushion plants, and lianas (Figure 13.4D). In turn, a wide array of habitats is occupied by species of these two genera. *Dubautia* habitats range from the wettest known on earth on Mount Wai'ale'ale, Kaua'i, and Pu'u Kukui, West Maui, to semiarid on the leeward southerly slopes of the two youngest islands, Maui and Hawai'i. In addition to this ecological diversity, *Dubautia* and

FIGURE 13.1. The Haleakala silversword (*Argyroxiphium sandwicense* subsp. *macrocephalum*), a monocarpic acaulescent rosette plant. (A) Habit of flowering plant; (B) capitulum (radiate). Reproduced from Wagner et al. (1990), courtesy of Bishop Museum Press, Bishop Museum, Honolulu, Hawai'i.



Wilkesia species exhibit extreme variation in leaf anatomical characteristics. Leaf venation ranges from highly reticulate, in the mesophytic liana *Dubautia latifolia*, to strictly parallel with few cross-connecting veinlets in the fibrous-leaved, xerophytic rosette plant *Wilkesia gymnoxiphium* (Carlquist, 1959b; Carr, 1985).

Despite the wide morphological and ecological variation found within the silversword alliance, cytogenetic (Carr and Kyhos, 1981, 1986), isozymic (Witter, 1986; Witter and Carr, 1988), and chloroplast DNA (cpDNA) (Baldwin, 1989; Baldwin et al., 1990, 1991) investigations indicate monophyly of this group. Previous to these studies, Carlquist (1959a) determined that most of the morphological and anatomical features that unite these Hawaiian Islands plants are shared with members of subtribe Madiinae (Heliantheae), a group of about 85 herbaceous or suffrutescent species in 14 genera, popularly known as tarweeds, that occur primarily within the California Floristic Province (hereafter abbreviated "California FP," as distinct from the state of California) (Howell, 1957; Raven and Axelrod, 1978). These shared characteristics included several details of head architecture and leaf anatomy that define the tarweed group. On this basis, Carlquist (1959a) concluded that the

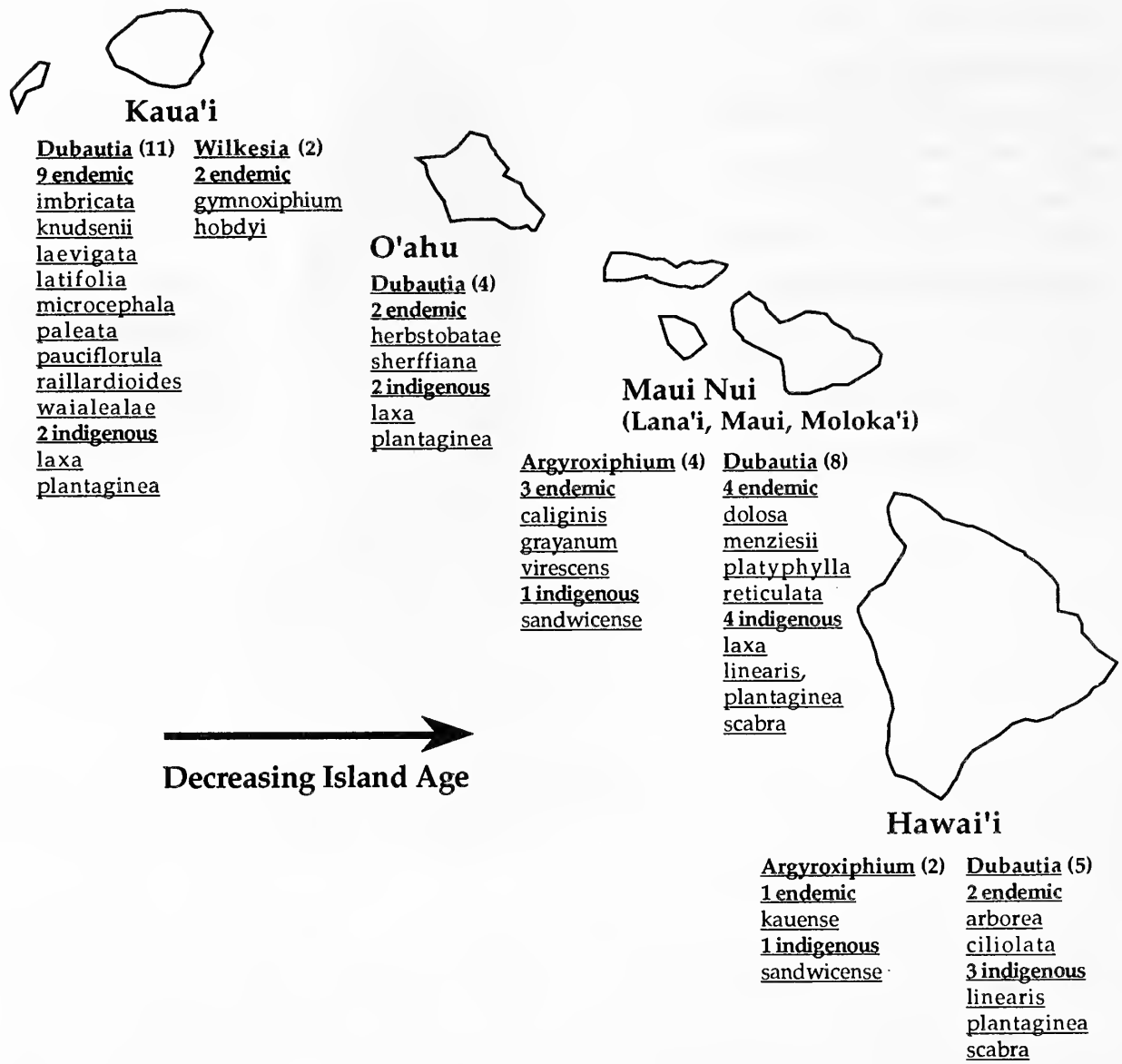
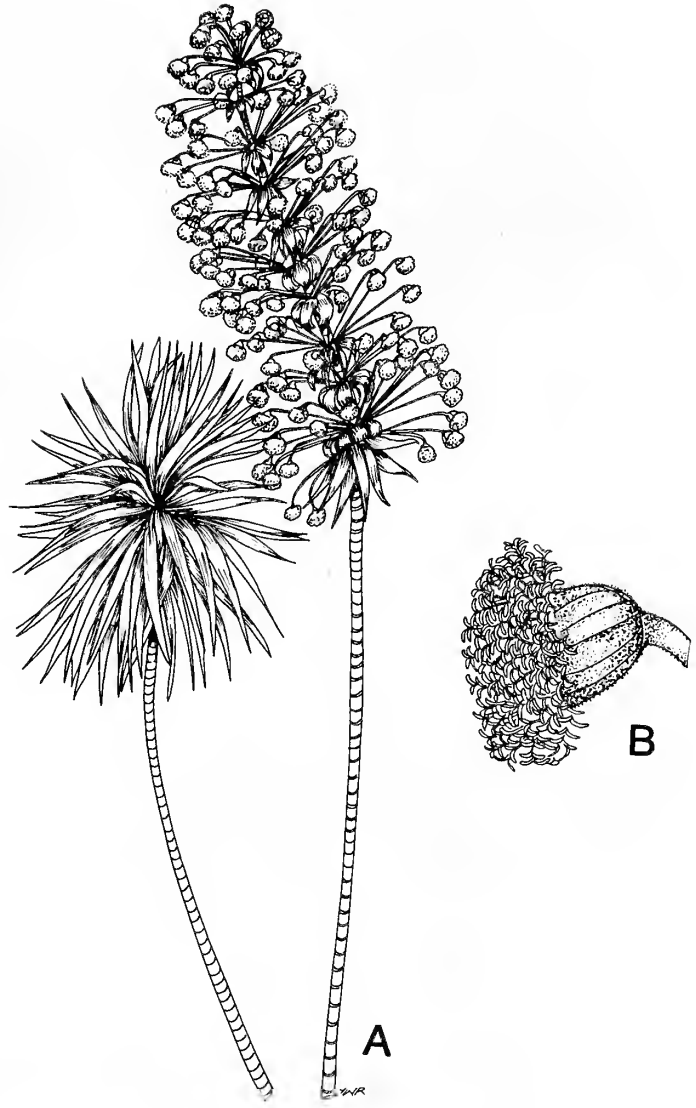


FIGURE 13.2. Distribution of silversword alliance species in the Hawaiian archipelago. Total number of species per genus on each island or island group is indicated in parentheses. Listed below each genus are the specific epithets of the endemic species and the indigenous but not endemic species (i.e., those found on at least one other island or island group). The islands of Kaho‘olawe (not shown), Lana‘i, Maui, and Moloka‘i, which are situated on a common platform and were connected during periods of lowered sea level, constitute a single biogeographic unit (see Carson and Clague, this volume, Chapter 2).

Hawaiian Islands species belonged to subtribe Madiinae and originated from American tarweeds. This hypothesis was strongly reinforced by cpDNA results (Baldwin, 1989; Baldwin et al., 1991).

In this chapter, the historical biogeography and ecology of the silversword alliance are re-examined based on molecular phylogenetic data from 18–26S nuclear ribosomal DNA (nrDNA) sequences of the internal transcribed spacer (ITS) region (Baldwin, 1992; B.G. Baldwin, unpubl.). Biogeographic patterns, founder events, and habitat shifts in

FIGURE 13.3. The *iliau* (*Wilkesia gymnoxiphium*), a monocarpic caulescent rosette plant. (A) Habit of plants in vegetative (*left*) and flowering (*right*) condition; (B) capitulum (discoid). Reproduced from Wagner et al. (1990), courtesy of Bishop Museum Press, Bishop Museum, Honolulu, Hawai'i.



this remarkable Hawaiian Islands group are reassessed from patterns of speciation suggested by the ITS trees. In addition, molecular evidence that indicates origin of the silversword alliance from an extant California FP tarweed lineage is reviewed (Baldwin, 1989, 1991, 1992, 1993a; Baldwin et al., 1991) and discussed in the light of new evidence herein.

MATERIALS AND METHODS

nrDNA ITS sequences were analyzed from most of the same total DNAs examined in earlier cpDNA studies (Baldwin, 1989; Baldwin et al., 1990, 1991) and a few additional accessions (Table 13.1). Sampling included 25 of the 28 silversword alliance species; tissues of *Dubautia dolosa* (Degener & Scherff) G. Carr and *D. waialealae* Rock were unavailable, and *Argyroxiphium virescens* Hillebr. may be extinct. California FP tarweed sampling excluded two published sequences from *Madia elegans* D. Don

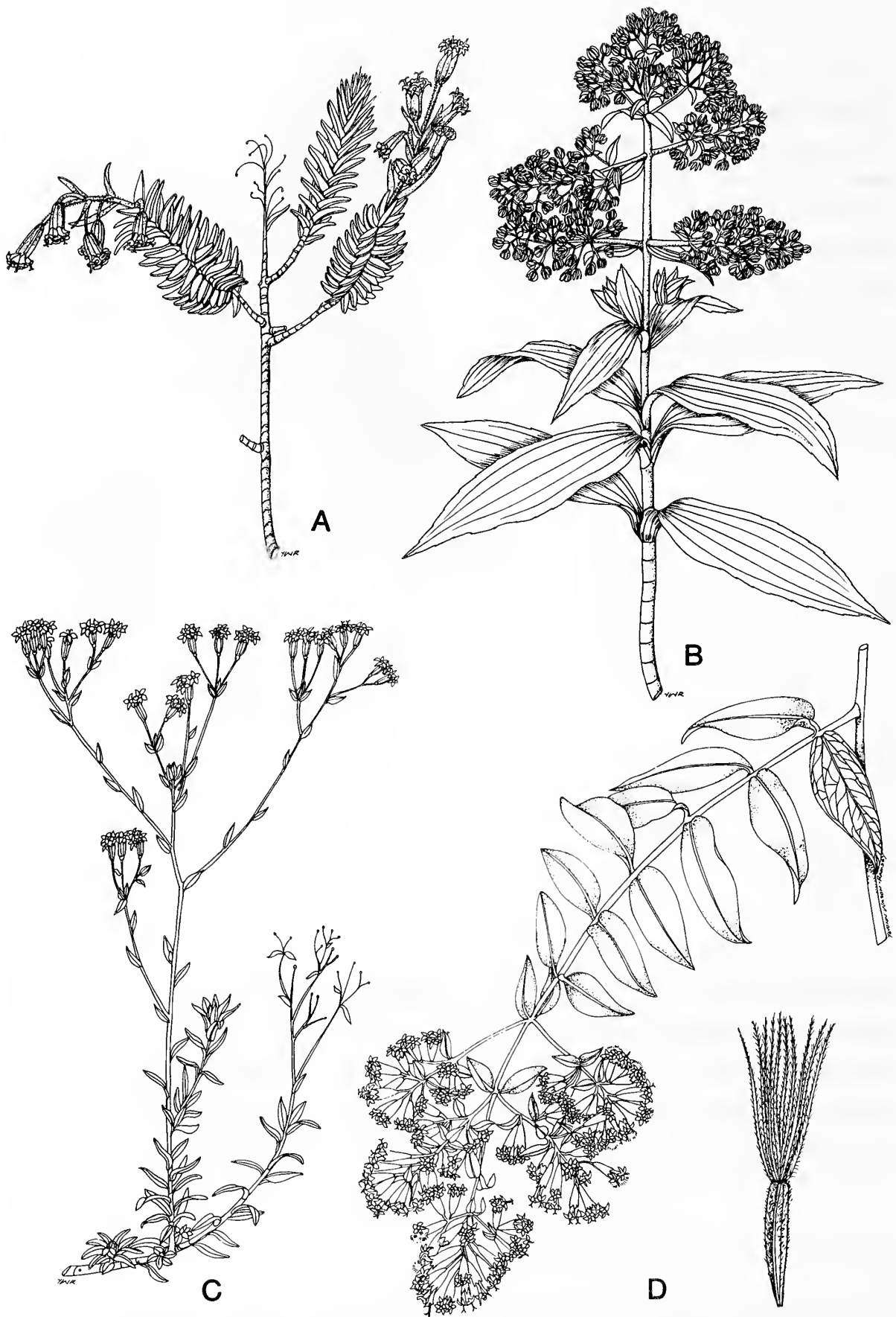


FIGURE 13.4. Flowering branches of *Dubautia* species, showing leaf arrangement and size, and capitulescence form. (A) *D. ciliolata* subsp. *ciliolata*, a xerophytic shrub; (B) *D. plantaginea* subsp. *plantaginea*, a mesophytic shrub; (C) *D. scabra* subsp. *scabra*, a mesophytic subshrub; (D) *D. latifolia*, a mesophytic liana, showing achene (disk) and pappus. Reproduced from Wagner et al. (1990), courtesy of Bishop Museum Press, Bishop Museum, Honolulu, Hawai'i.

and *M. stebbinsii* T. W. Nelson & J. P. Nelson (Baldwin, 1992) because their inclusion introduced alignment ambiguities that required deletion of sites with potential information about silversword alliance phylogeny. A more comprehensive sampling of *Madia*, including these two sequences, alleviated this problem (Baldwin, 1993a) but is beyond the scope of this chapter.

Asymmetric polymerase chain reaction (PCR) amplifications and direct sequencing of ITS 1, ITS 2, and all or most of the 5.8S subunit followed Baldwin (1992, 1993b). Primers "ITS5" and "ITS2" (White et al., 1990) were used to amplify and sequence the ITS 1 spacer and part of the 5.8S region. Primers "ITS3" and "ITS4" (White et al., 1990) allowed amplification and sequencing of the ITS 2 spacer and most of the remainder of the 5.8S region. Complete 5.8S sequences were obtained by amplifying the entire ITS region with primers "ITS5" and "ITS4" and sequencing from either end. Although rates of nucleotide sequence evolution are much higher in the spacers (i.e., ITS 1 and ITS 2) than in the 5.8S subunit (Baldwin, 1992, 1993b), these three units are contiguous and constitute the "ITS region" (Baldwin, 1992, 1993b). For this reason, combined data from all three units are hereafter referred to simply as "ITS" data.

Phylogenetic analyses of ITS data were conducted using the maximum-parsimony algorithm in PAUP version 3.1.1 (Swofford, 1993). The PAUP heuristics option and 20 random addition sequences of the taxa were implemented, with TBR branch swapping and collapse of zero-length branches, to find the minimum-length trees. Rooting of ITS trees was by global parsimony using two outgroup species outside Madiinae, *Arnica mollis* and *Hulsea algida* (Table 13.1). All character states were treated as unordered, and all characters and character states were assigned equal weight. Gaps in nucleotide alignments were treated as missing data. Bootstrap values for lineages were calculated from 100 replicate parsimony analyses using the PAUP heuristics option and closest addition sequence of the taxa. The decay index (Bremer, 1988; Donoghue et al., 1992) of each lineage (i.e., the number of additional steps required to obtain a resolution inconsistent with a clade in at least one of the maximally parsimonious trees) was determined for tree lengths up to two steps longer than the minimum-length trees.

Historical biogeographic patterns and ecological shifts were assessed using the character evolution algorithm in MacClade version 3.01 (Maddison and Maddison, 1992). These reconstructions were made for each maximally parsimonious ITS tree, with geographic distribution (i.e.,

island occurrence) and ecological distribution (i.e., habitat occurrence) of terminal taxa treated as characters. All character states were treated as unordered and were assigned equal weight. Ancestral nodes were constrained to single states (not polymorphic). Four islands or island groups (Kaua'i, O'ahu, Maui Nui complex, and Hawai'i) were used as character states in the biogeographic analysis (see Figure 13.2, Table 13.1). Two major habitat classes (dry and wet) were used as character states in the ecological analysis. Dry habitats typically receive less than 1,200 to 1,400 mm annual precipitation, with a pronounced dry season. Vegetation in dry habitats includes dry grasslands, shrublands, and forests (Gagné and Cuddihy, 1990). Wet habitats typically receive more than 1,200 to 1,400 mm annual precipitation and lack a pronounced dry season. Vegetation in wet habitats includes wet sedgeland, mixed communities, shrublands, and forests (Gagné and Cuddihy, 1990). It also includes the mesic forests and most of the mesic shrublands of Gagné and Cuddihy (1990), although some of the latter fall under the dry habitats used here. Character state assignments were based on the most common habitat occurrences of taxa, which allowed for unambiguous assignments in all cases.

RESULTS

nrDNA ITS Analyses

A matrix of 656 characters was necessary to align all 43 ITS sequences. Alignment required insertion of gaps at 27 (4.1% of) sites. No indications of infragenomic length variants or major sequence variants were found in any of the PCR products or nucleotide sequences.

Seven sites (61, 62, 74, 75, 244, 464, 465; see Appendix 13.1) were eliminated from consideration in the phylogenetic analysis because of alignment ambiguities. None of these seven sites included potential phylogenetic information within the silversword alliance. A data matrix of 118 potentially informative sites was obtained after removal of these problematic characters (Appendix 13.1). Phylogenetic analysis of the silversword alliance ITS sequences, together with continental Madiinae and outgroup species, resulted in two minimum-length trees of 230 steps, each with a consistency index (CI) of 0.67 and a retention index (RI) of 0.85, excluding sites without potential phylogenetic information. The strict consensus of these trees is shown in Figure 13.5. These trees differ

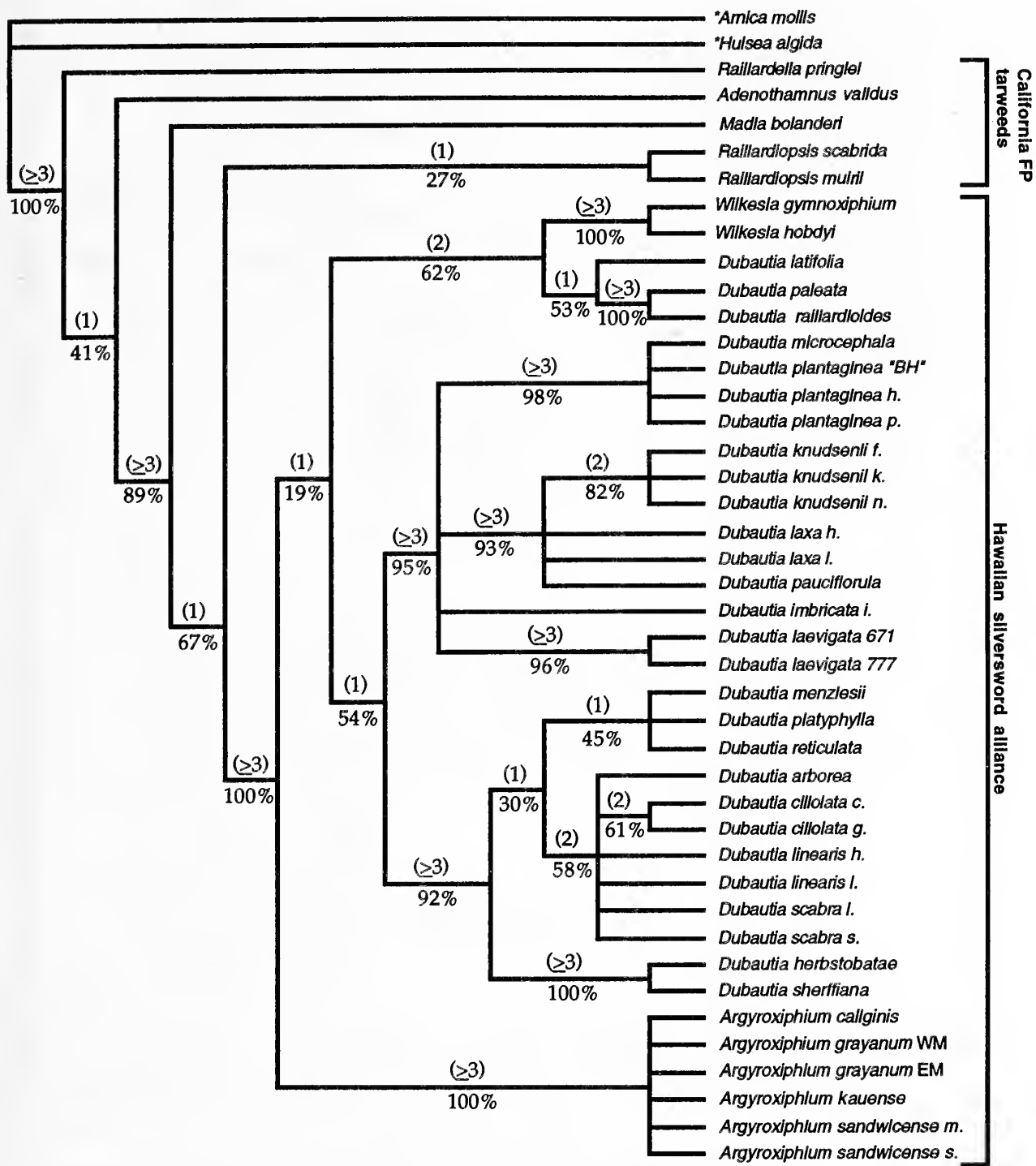


FIGURE 13.5. Strict consensus of two maximally parsimonious trees based on 18–26S nrDNA ITS sequence variation in representatives of 25 silversword alliance species in *Argyroxiphium*, *Dubautia*, and *Wilkesia*; 5 California FP tarweeds in *Adenothamnus*, *Madia*, *Raillardella*, and *Raillardiopsis*; and 2 out-group species outside Madiinae, marked by asterisks (*Arnica mollis* and *Hulsea algida*) (see Table 13.1). CI, 0.67; RI, 0.85. Percentages below branches are bootstrap values from 100 replicate runs. Numbers in parentheses above branches are decay index values. Bootstrap and decay index values were obtained using the PAUP heuristics option, with closest addition sequence of taxa.

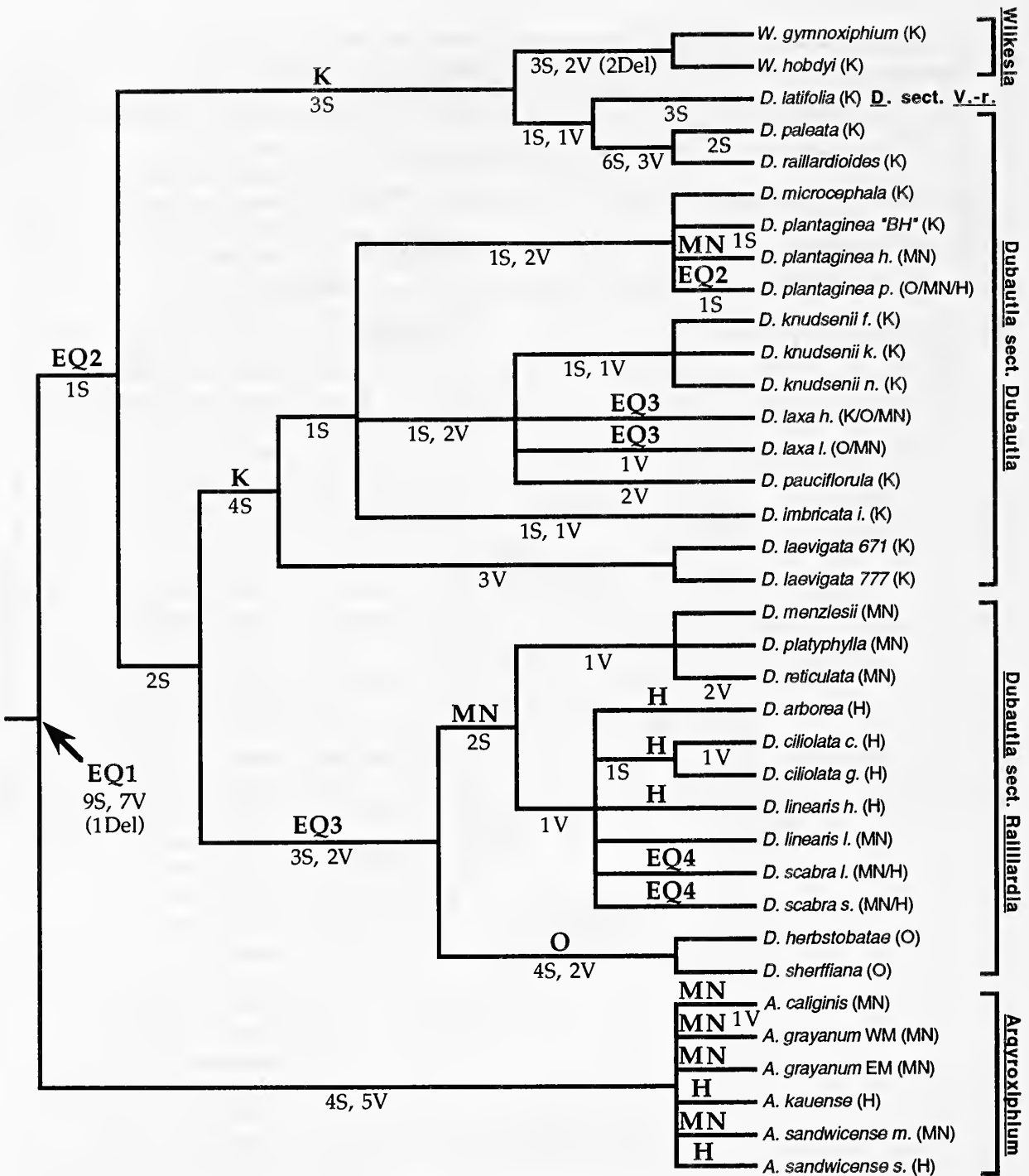


FIGURE 13.6. Portion of one of the two maximally parsimonious trees based on 18–26S nrDNA ITS sequence variation, showing only the silversword alliance lineage. Numbers of character changes mapped to each branch, using ACCTRAN optimization in PAUP, are indicated below each branch as transitions (S) or transversions (V). Deletion mutations (Del), not included in the phylogenetic analysis, are indicated below branches in parentheses: The two deletions that define *Wilkesia* are at sites 108 to 109 and 615 to 616 in the aligned matrix of 43 sequences; the deletion that defines the silversword alliance is at site 476. Bold letters above branches are island or island group abbreviations that indicate the geographic origin of the lineage defined by that node, based on MacClade 3.01 reconstructions. An island or island group abbreviation within a polytomy or following an equivocal branch represents the point at which the ancestral occurrence on that island or island group is unequivocal; the actual

only in transposed placement of *Dubautia laevigata* and *D. imbricata*. Pairwise nucleotide sequence divergence between ITS sequences of silversword alliance species ranged from 0 to 4.5%. Pairwise ITS sequence divergence between silversword alliance and California tarweed taxa ranged from 5.6 to 10.5% of nucleotides. Bootstrap values for ITS lineages resolved in all minimum-length trees ranged from 19 to 100%, with 95% or greater support for 9 of the 24 clades. Within the silversword alliance ITS lineage, 5 clades decayed in trees one step longer than minimum, 4 clades decayed in trees two steps longer than minimum, and 10 clades (including the branch supporting monophyly of the Hawaiian Islands species) required three or more steps to decay. Internal branch lengths (i.e., numbers of character changes along branches that define relationships) within the silversword alliance ITS trees ranged from one to nine changes among the sublineages (Figures 13.6 and 13.7). Sixteen changes marked the ITS branch that defines the Hawaiian Islands group. In addition, three length mutations with potential phylogenetic information were detected in the silversword alliance ITS lineage (Figures 13.6 and 13.7). Although none of these deletions was used in the phylogenetic analysis, all three were mapped onto the site-substitution-based trees with no homoplasy.

Biogeographic Reconstructions

Reconstruction of the historical biogeography of silversword alliance lineages is shown for one of the minimum-length ITS trees in Figure 13.6, which includes only the Hawaiian Islands taxa. Ancestral reconstruction in the other ITS tree was identical. These estimates indicate the following: (1) each of the two major lineages that together include all Kaua'i *Dubautia* and *Wilkesia* species descended from a Kaua'i ancestor; (2) *D. herbstobatae* and *D. sherffiana* shared a common ancestor on O'ahu;

←

founder event may precede such branches with additional resolution of the polytomy or of deeper branches. Within polytomies, the changes (from the ancestral state) indicated are only those that follow unequivocal branch reconstructions and where more than one geographic state exists among the taxa. Letters in parentheses following species names indicate where those species occur. Abbreviations are K, Kaua'i; O, O'ahu; MN, Maui Nui; H, Hawai'i; EQ1, California FP or Kaua'i or Maui Nui or Hawai'i; EQ2, Kaua'i or Maui Nui; EQ3, Kaua'i or O'ahu or Maui Nui; EQ4, Maui Nui or Hawai'i; *D. sect. V.-r.*, *Dubautia* section *Venoso-reticulatae*.

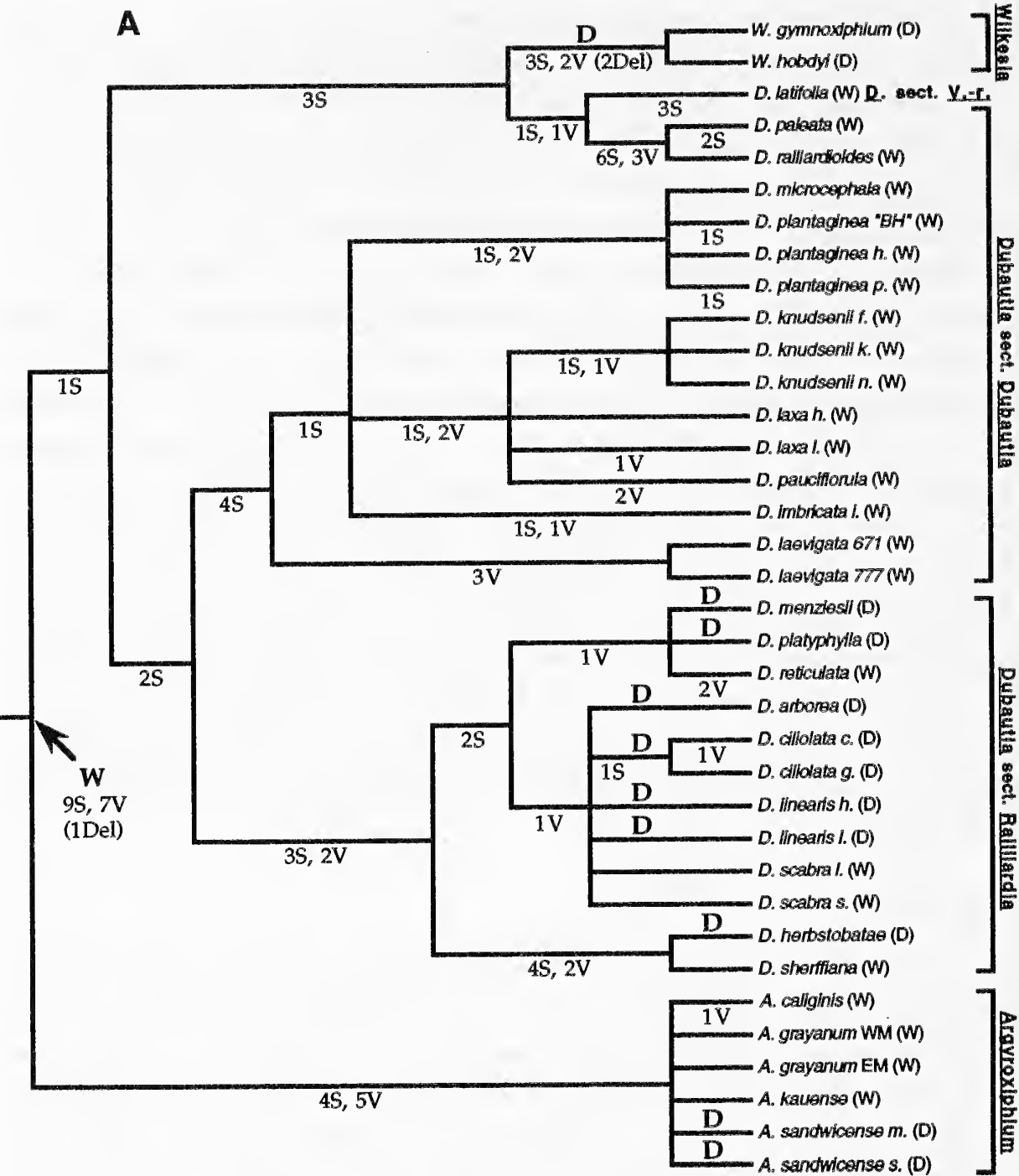


FIGURE 13.7. (A) Portion of one of the two maximally parsimonious trees based on 18–26S nrDNA ITS sequence variation, showing only the silversword alliance lineage. Numbers of character changes mapped to each branch, using ACCTRAN optimization in PAUP, are indicated below branches as transitions (S) or transversions (V). Deletion mutations (Del), not included in the phylogenetic analysis, are indicated below branches in parentheses: The two deletions that define *Wilkesia* are at sites 108 to 109 and 615 to 616 in the aligned matrix of 43 sequences; the deletion that defines the silversword alliance is at site 476. Bold letters above branches are habitat abbreviations that indicate the ancestral habitat of the lineage defined by that node, based on MacClade 3.01 reconstructions. A habitat abbreviation within a polytomy (or following an equivocal branch) represents the point at which the ancestral habitat occurrence is unequivocal; the actual habitat shift may precede such branches with additional

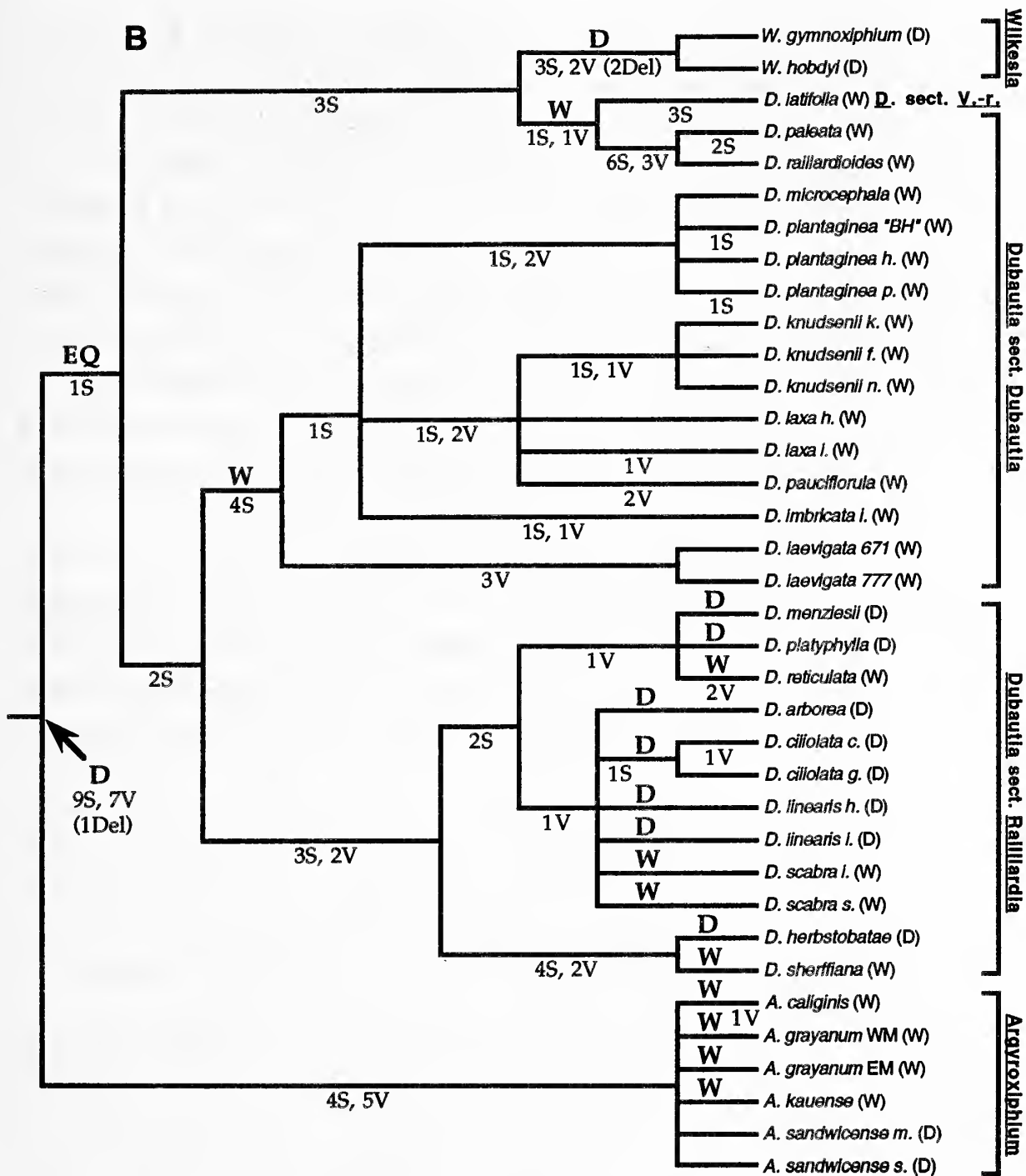


FIGURE 13.7. (Continued)

resolution of the polytomy (or of deeper branches). Within polytomies, the changes (from the ancestral state) indicated are only those that follow unequivocal branch reconstructions and where more than one habitat state exists among the taxa. Letters in parentheses following species names indicate habitats in which those species occur. Abbreviations are W, wet habitat; D, dry habitat; EQ, wet or dry habitat; D. sect. V-r., *Dubautia* section *Venoso-reticulatae*. Designation of W for the basalmost branch indicates only that the silversword alliance ancestor occurred in a wet habitat; the habitat shift occurred at a deeper branch in the ITS tree, based on the reconstruction. (B) Reconstruction that assumes that the silversword alliance ancestor occupied a dry habitat (see text). Abbreviations are the same as for (A).

and (3) all *Dubautia* section *Railliardia* (see Table 13.1 and Figures 13.6 and 13.7 for sectional limits) species on Maui Nui and Hawai'i originated from a Maui Nui ancestor. Ambiguous reconstructions were obtained for ancestors of the silversword alliance (California FP, Kaua'i, Maui Nui, or Hawai'i), *Argyroxiphium* (California FP, Kaua'i, Maui Nui, or Hawai'i), *Dubautia*-*Wilkesia* (Kaua'i or Maui Nui), *Dubautia* exclusive of *D. latifolia*, *D. paleata*, and *D. raillardoides* (Kaua'i or Maui Nui), and *Dubautia* section *Railliardia* (Kaua'i, O'ahu, or Maui Nui). Occurrence of the California FP in the within-archipelago reconstructions is an artifact of equal weighting of all character states (geographic sites); dispersal between the California FP and any of the Hawaiian Islands probably should receive greater weight than inter-island dispersal because of major distance disparities.

Fewer ambiguities in biogeographic reconstructions of internal nodes were obtained by assuming each of the three possible within-archipelago sites of silversword alliance origin. Reconstructions assuming either a Kaua'i or Hawai'i origin of the silversword alliance indicate a Kaua'i origin of *Dubautia*-*Wilkesia*. An enforced Hawai'i origin of the silversword alliance suggests, in addition, an unequivocal Hawai'i origin of *Argyroxiphium*. In contrast, under the assumption of a Kaua'i origin of the silversword alliance, the ancestry of *Argyroxiphium* remained equivocal (Kaua'i, Maui Nui, or Hawai'i). Enforced Maui Nui origin of the silversword alliance resulted in an unambiguous Maui Nui origin of *Argyroxiphium*, but the origin of *Dubautia*-*Wilkesia* remained equivocal (Kaua'i or Maui Nui).

Nearly complete resolution of biogeographic relationships was obtained from an alternative biogeographic reconstruction based on slightly modified ITS trees that included a hypothetical extinct Kaua'i *Argyroxiphium* sister group of modern silversword and greensword species (see "Biogeographic History of the Silversword Alliance"). These results dictate that each of the following groups originated from a common Kaua'i ancestor: the silversword alliance, *Argyroxiphium*, *Dubautia*-*Wilkesia*, and each of the two Kaua'i lineages of *Dubautia* and *Wilkesia* species. The ancestral sites of origin of *Dubautia* section *Railliardia* (Kaua'i, O'ahu, or Maui Nui) and extant *Argyroxiphium* species (Kaua'i, Maui Nui, or Hawai'i) remained ambiguous under this assumption.

Ecological Reconstructions

Reconstruction of the historical ecology of silversword alliance lineages is shown for one of the minimum-length ITS trees in Figure 13.7A, which includes only the Hawaiian Islands taxa. Ancestral reconstruction in the

other ITS tree was identical. This resolution suggests that at least five ecological shifts from wet to dry habitats occurred during the diversification of the silversword alliance. These wet-to-dry changes include at least one in *Argyroxiphium*, one in the *Wilkesia gymnoxiphium*–*W. hobdyi*–*Dubautia latifolia*–*D. paleata*–*D. raillardioides* lineage and three in *Dubautia* section *Railliardia*.

In contrast to near biogeographic uniformity among the continental taxa (i.e., all but one species [*Hemizonia streetsii* A. Gray] occur primarily in the California FP), ecological variation exists within this group. Inclusion of many unsampled (primarily California FP) *Madia* species in the phylogenetic analysis could potentially alter ecological reconstruction of the silversword alliance ancestor. This possibility warranted exploration of the consequences of a dry-habitat silversword alliance ancestor. Under this assumption, at least six shifts between dry and wet habitats occurred (Figure 13.7B). Although the direction of change was ambiguously resolved in most of these cases, at least one of the shifts in *Argyroxiphium* and one in *Dubautia*–*Wilkesia* were from dry to wet habitats.

MONOPHYLY AND ANCESTRY OF THE SILVERSWORD ALLIANCE

Phylogenetic Evidence

Both monophyly and a tarweed (Heliantheae, subtribe Madiinae) ancestry of the silversword alliance are reinforced by phylogenetic analysis of nrDNA ITS data (see Figure 13.5) (Baldwin, 1992), in agreement with earlier cpDNA findings (Baldwin, 1989; Baldwin et al., 1991). Further, the ITS trees corroborate cpDNA evidence (Baldwin, 1989; Baldwin et al., 1991) that species in *Madia* and *Raillardiopsis* are more closely related to the Hawaiian Islands taxa than to other California FP tarweeds in *Adenothamnus* and *Raillardella* (Baldwin, 1992). In fact, a preliminary ITS phylogeny including representatives of all 17 Hawaiian Islands and California FP Madiinae genera suggests that *Madia* and *Raillardiopsis* are the closest living relatives of the Hawaiian Islands species (Baldwin, 1991; B. G. Baldwin, unpubl.).

Production of vigorous transoceanic hybrids between silversword alliance species and each of the tarweeds *Madia bolanderi* and *Raillardiopsis muirii* (Baldwin, 1989; Kyhos et al., 1990; Baldwin et al., 1991) suggests close genetic similarity between these Hawaiian Islands and California FP plants, in accord with their close phylogenetic relationship.

Unfortunately, lack of meiotic chromosomal association in these hybrids hinders assessment of structural genomic relationships.

Biogeographic Source Area of the Silversword Alliance

The California FP is suggested as the source area of the silversword alliance by the near restriction of continental Madiinae, including *Madia* and *Raillardiopsis*, to this region (Howell, 1957; Raven and Axelrod, 1978). Except for the Hawaiian Islands representatives, only one species of Madiinae is found exclusively outside of the California FP: *Hemizonia streetsii*, an insular Baja California endemic, which is part of a large, otherwise California FP genus (Raven and Axelrod, 1978). Within *Madia* and *Raillardiopsis*, the only species with ranges that extend far outside the California FP are self-compatible members of *Madia*. Unlike these wide-ranging *Madia* taxa, many silversword alliance species possess sporophytic self-incompatibility, including members of all three Hawaiian Islands genera (Carr et al., 1986). Genetic complexity of sporophytic self-incompatibility militates against reconstituting this function once lost (Mulcahy, 1984), thus making the widespread *Madia* species, including the South American populations, unlikely candidates for direct ancestors of the Hawaiian Islands group.

The actual mainland ancestor of the Hawaiian Islands species is probably extinct. All members of the silversword alliance are polyploid with $n = 14$ or 13 (Carr and Kyhos, 1986; Witter, 1986; Witter and Carr, 1988). In *Madia* and *Raillardiopsis*, the only known polyploids are a subset of the self-compatible *Madia* species (Keck, 1959; Kyhos et al., 1990) discussed above as improbable ancestors of the Hawaiian Islands taxa. These *Madia* polyploids each exhibit a suite of floral character states that suggests predominant selfing. The possibility cannot be ruled out, however, that polyploidy in the Hawaiian Islands group arose in situ (e.g., by autopolyploidy). Critical evidence about the origin of polyploidy in the silversword alliance may result from genomic comparisons of the Hawaiian Islands species with the mainland perennials *R. scabrida* and *M. madioides* (Nutt.) E. Greene, the only $n = 7$ species in *Madia* and *Raillardiopsis*.

Transoceanic Dispersal

Migration of the silversword alliance ancestor from North America to the Hawaiian Islands required a dispersal event of intercontinental magnitude, across at least 3,900 km of open ocean. Pacific Basin geology provides no evidence of extinct islands that could have provided signifi-

cant stepping-stones for dispersal across this immense barrier. The distance between North America and the Hawaiian Islands was, in fact, even greater in prehistory. Progressive expansion of the mid-Atlantic Ridge has gradually displaced North America westward toward the relatively stationary Hawaiian hot spot (Dalrymple et al., 1973; Wilson, 1976; Clague and Dalrymple, 1987; see also Carson and Clague, this volume, Chapter 2).

External bird transport appears to be the only feasible mode by which dispersal between North America and the Hawaiian Islands could have occurred. The thin, dry achene walls of tarweeds are almost certainly not resistant to bird digestive fluids or seawater. These fruits are also too large and lacking in buoyancy to be carried great distances by normal wind currents (cf. Carlquist, 1966, 1967).

Both fruit types of tarweeds exhibit obvious adaptations for animal dispersal (Carlquist, 1966, 1967). In the California FP and Hawaiian Islands groups, ray achenes are, in general, enveloped partially or completely by the lateral margins of the involucre bracts (Keck, 1959; Carr, 1985). In most radiate species of *Madiinae*, these bracts are covered with sticky glandular trichomes that promote strong adhesion of the bract/fruit disseminule to fur or feathers. Disk achenes of *Raillardiopsis*, *Dubautia*, and several *Madia* species, including *M. bolanderi*, are covered with stiff, upwardly appressed hairs and are crowned by a pronounced plumose pappus (i.e., a tuft of flattened, fringed bristles or awns) (see Figure 13.4D). The pointed tips of these disk fruits can readily penetrate fur or feathers but are difficult to extract because of resistance from the achene hairs and pappus. Inter-island migration of *Dubautia* species (see below), all of which lack ray flowers, demonstrates the effectiveness of these disk fruits as agents of long-distance dispersal. Also, repeated documentation of migratory and accidental North American bird species in the Hawaiian Islands (Pratt et al., 1987) indicates the potential for transoceanic avian transport of tarweeds.

The possibility that ray fruits may have been involved in the original tarweed dispersal to the Hawaiian Islands is reinforced by phylogenetic evidence that both ray and disk flowers were present in the ancestor of the silversword alliance. Character evolution reconstructions based on the minimum-length ITS trees suggest that presence of ray flowers, as in *Argyroxiphium*, was the ancestral condition in the silversword alliance and that a single loss of rays occurred in the ancestor of *Dubautia-Wilkesia*. This is true even if *Raillardiopsis muirii*, the sole discoid species in *Madia-Raillardiopsis*, is the closest relative to the silversword alliance among the California FP species included in this study, as suggested by

the cpDNA trees (Baldwin, 1989; Baldwin et al., 1991) and previous ITS analyses that included additional *Madia* species (Baldwin, 1992, 1993a). These last-mentioned ITS data also suggest that annual, radiate *Madia* species, not included in the present study (see Materials and Methods section), are the closest living relatives of *R. muirii*. Assuming such close relationship between radiate *Madia* species and *R. muirii*, reconstructions based on such modified ITS trees indicate presence of ray flowers in the silversword alliance ancestor. The existence of multiple loci governing ray presence in other tarweeds of the genus *Layia* (Ford and Gottlieb, 1990) suggests that reacquisition of ray flowers once lost would be more unlikely than independent losses of ray flowers in different lineages.

Breeding Barrier to Dispersal

Establishment of the ancestral Hawaiian Islands founder species remains the most puzzling question about the origin of the silversword alliance. As mentioned above, the silversword alliance ancestor apparently possessed sporophytic self-incompatibility, making this group a prominent exception to Baker's Rule (Baker, 1955, 1967; Carr et al., 1986). Pollination studies indicate minimal selfing or "leakiness" in the self-incompatible silversword alliance species that have been tested (Carr et al., 1986). These data suggest that the original founder event to the Hawaiian Islands involved either (1) multiple individuals of different parentage that were simultaneously dispersed to the same location or (2) at least one perennial individual that underwent either vegetative propagation or highly limited selfing while accumulating S-allele mutations necessary to resume efficient sexual reproduction (see Carr et al., 1986, for detailed discussion). Two self-incompatible perennials in *Madia* and *Raillardiop-sis* (*M. bolanderi* and *R. muirii*) are, in fact, capable of vegetative reproduction. Absence of annual *Madia* species in the analyses presented herein prohibits assessment of the differential likelihood of a perennial or annual ancestry of the silversword alliance based on the ITS trees.

BIOGEOGRAPHIC HISTORY OF THE SILVERSWORD ALLIANCE

Background

Carr et al. (1989) inferred that the original founder event that gave rise to the silversword alliance occurred on Kaua'i. In their model, inter-island

species dispersal proceeded in a predominantly southeastward direction from the oldest modern high island, Kaua'i, to progressively newer islands as they emerged from the Hawaiian Islands hot spot and were rafted to the northwest. A similar general pattern of colonization has been reconstructed for other highly diversified Hawaiian Islands lineages, most notably for endemic *Drosophila* (Carson, 1983a; see Carr et al., 1989, for comparison with the silversword alliance).

Site of Origin within the Archipelago

Two reasons for assuming a Kaua'i (or older, extinct island) origin of highly diversified organismal lineages that span the high Hawaiian Islands are (1) the expectation that probability of colonization and species radiation is greatest at island formation and decreases with increasing island age, and (2) the inference that such endemic lineages are likely to be older than O'ahu, Maui Nui, and Hawai'i. Although the first argument is compelling, direct evidence of geographic origin from a rooted phylogeny relies only on data from the organisms and therefore is based on fewer assumptions.

Equivocal resolution of the geographic site of origin of the silversword alliance based on the ITS trees (see Figure 13.6) is attributable to the sister-group relationship between *Argyroxiphium* and *Dubautia-Wilkesia*. Exclusion of *Argyroxiphium* from the phylogeny resulted in an unequivocal Kaua'i origin of the *Dubautia-Wilkesia* lineage, as expected from the position of the younger island endemic lineage (*Dubautia* section *Railliardia*) within the non-monophyletic Kaua'i group. Exclusion of *Dubautia-Wilkesia* from the ITS trees resulted in an equivocal California FP, Maui Nui, or Hawai'i origin of the remaining species (i.e., those in *Argyroxiphium*), as expected from the lack of phylogenetic resolution within this Maui Nui and Hawai'i lineage.

Expectation of a Kaua'i (or pre-Kaua'i) origin of the silversword alliance based on the geologic and group-age assumptions mentioned above is, therefore, unrealized because of the basal phylogenetic position of *Argyroxiphium*. Incorrect resolution of relationships among the four main silversword alliance ITS lineages (i.e., *Argyroxiphium*, *Wilkesia-Dubautia latifolia*-*D. paleata*-*D. raillardioides*, remaining Kaua'i *Dubautia* species, and *Dubautia* section *Railliardia*) could explain this result, based on weak support for the two pertinent phylogeny branches. The sister-group relationship between *Argyroxiphium* and *Dubautia-Wilkesia* was also obtained, however, from analyses of combined cpDNA data

(Baldwin, 1989; Baldwin et al., 1990, 1991) and ITS results (B. G. Baldwin, unpubl.). Inadequate resolution was obtained from analyses of the cpDNA data alone to address this question.

There is no physical evidence to indicate that members of *Argyroxiphium* ever occurred anywhere but the two youngest islands, Maui and Hawai'i. Restriction of *Argyroxiphium* species to high-elevation habitats might offer a clue to the absence of members of this genus on the highly eroded, older islands of Kaua'i and O'ahu. There are, however, large high-elevation bogs on Kaua'i, (e.g., on Mount Wai'ale'ale) that appear similar superficially to bogs that provide habitat for *A. caliginis* and *A. grayanum* in the West Maui Mountains.

Comparison of branch lengths within the *Argyroxiphium* ITS lineage (see Figure 13.6 or 13.7) (i.e., of numbers of mutations along phylogeny branches) may provide additional insight into the biogeographic history of this genus. The long branch that supports monophyly of *Argyroxiphium* is in sharp contrast to the almost complete identity of ITS sequences among *Argyroxiphium* species. Assuming that the probability of species radiation is greatest on island formation and decreases with increasing island age, this contrast may indicate a long evolutionary history of *Argyroxiphium* on an older island such as Kaua'i, followed by dispersal to, and recent radiation on, the youngest islands, Maui and Hawai'i.

Assuming an extinct Kaua'i *Argyroxiphium* sister group to modern silversword and greensword species removed most of the basal ambiguity from biogeographic reconstructions based on the ITS trees. This single change resulted in the resolution of Kaua'i ancestry for the silversword alliance and all the main lineages therein except *Dubautia* section *Railliardia*, the site of origin of which remains ambiguous (Kaua'i, O'ahu, or the Maui Nui complex). Reconstructions under the Kaua'i *Argyroxiphium* assumption indicate multiple founder events on each of the younger islands by prehistoric members of the silversword alliance but no evident recolonizations of Kaua'i, the most geographically isolated high island in the archipelago.

In the absence of assumptions about extinct *Argyroxiphium* species, Maui Nui and Hawai'i origins of the silversword alliance were among the maximally parsimonious reconstructions from the ITS trees (see Figure 13.6). A Maui Nui origin would mean that the silversword alliance arose no more than ca. 2 million years ago (Ma); Hawai'i origin would dictate that the group arose no more than ca. 500 thousand years ago (ka) (Dalrymple et al., 1973; Clague and Dalrymple, 1987). Based on the ITS

trees, Maui Nui or Hawai'i origin of the silversword alliance dictates a young island origin only for *Argyroxiphium*; these assumptions both allow for origin of *Dubautia-Wilkesia* on Kaua'i, from a Maui Nui or Hawai'i to Kaua'i founder event, with subsequent migration to younger islands. It seems doubtful, however, that the spectacular radiation of *Dubautia-Wilkesia* on Kaua'i could have occurred after more than 3 million years of colonization of that island by other plant groups, given that Kaua'i was formed ca. 5.1 Ma (Dalrymple et al., 1973; Clague and Dalrymple, 1987).

Pre-Kaua'i Considerations

Extinct high islands of greater age than Kaua'i were not considered in the above reconstructions of biogeographic history because of ignorance about past species occurrences on those now highly eroded or sunken seamounts. Although absolute ages of the Hawaiian Islands have been determined (Dalrymple et al., 1973; Clague and Dalrymple, 1987), absolute time of origin of the silversword alliance is uncertain because of absence of a fossil record for Madiinae, undetermined rates of evolutionary change in ITS 1 and ITS 2, and the dispersed pattern of cpDNA restriction site mutations (Baldwin, 1989; Baldwin et al., 1990, 1991) among plastome regions with widely varying levels of interspecific variation. Most important, equivocal lineage-based reconstructions of young island colonizations prevented unambiguous age assignments to phylogeny nodes, a critical step in dating other branching points.

Assuming that the most recent common ancestor of modern silversword alliance species was endemic to a pre-Kaua'i island, biogeographic reconstructions based on the ITS trees indicate that a pre-Kaua'i origin of *Argyroxiphium* is among the maximally parsimonious solutions, whereas a Kaua'i origin of *Dubautia-Wilkesia* is unambiguously favored. Pre-Kaua'i ancestry of *Dubautia-Wilkesia* (i.e., an exclusively pre-Kaua'i distribution of the common ancestor of *Dubautia-Wilkesia*) would require that there were independent colonizations of Kaua'i by the ancestors of the two main Kaua'i ITS lineages. If independent founder events indeed account for the two Kaua'i *Dubautia-Wilkesia* lineages, then these clades are likely exceptional; none of the reconstructions based on the ITS trees unambiguously indicates speciation from more than one *Dubautia-Wilkesia* founder on any island, excluding subspeciation in *D. laxa* and *D. plantaginea*. If, however, the simplest phylogeny-based biogeographic hypothesis is correct, then the *Dubautia-Wilkesia* lineage had a common

ancestor on Kaua'i and therefore arose no earlier than Kaua'i (i.e., 5.1 Ma).

Dubautia-Wilkesia Reconstructions

Within *Dubautia-Wilkesia*, the ITS trees are compatible with the simplest hypothesis that only one colonization of each of the main islands resulted in speciation, ignoring subspeciation in *D. laxa* and *D. plantaginea* (see Figure 13.6). The sequence of young island colonizations was, however, resolved ambiguously by the molecular data. Maui Nui ancestry of the Hawai'i *Dubautia* endemics is supported by the ITS reconstructions but is provisional in lieu of phylogenetic resolution within this sublineage.

No unambiguous younger-to-older island founder events were reconstructed from the ITS trees. A Maui Nui-to-O'ahu back-dispersal of the ancestor of the *Dubautia herbstobatae*-*D. sherffiana* lineage is compatible with the ITS estimates (see Figure 13.6) and was suggested previously by Carr et al. (1989) based on allozyme results (Witter, 1986; Witter and Carr, 1988). As in *Argyroxiphium*, the possibility of Maui Nui colonization by Hawai'i species cannot be assessed without enhanced phylogenetic resolution in the Hawai'i *Dubautia* section *Railliardia* lineage, which includes Maui Nui *D. linearis* and *D. scabra*.

Concordance with Earlier Interpretations

Although founder event reconstructions based on ITS data are provisional because of weak support for basal internal branches, these estimates are highly congruent with previous conclusions based on cytogenetic, isozymic, and morphological data (Carr et al., 1989). Regardless of whether the silversword alliance originated on Kaua'i, Maui Nui, or Hawai'i, ITS results indicate a minimum of 13 inter-island founder events, as estimated by Carr et al. (1989). The ITS and earlier reconstructions of founder events are compatible except in two respects: (1) ITS estimates assume monophyly or paraphyly of subspecies, whereas Carr et al. (1989) allowed for polyphyly of subspecies, and (2) Carr et al. (1989) postulated that separate founder events accounted for each of the five Hawai'i *Dubautia* species, whereas the ITS trees indicate that three of these species (*D. arborea*, *D. ciliolata*, and either *D. linearis* or *D. scabra*) may have arisen from a single founder event.

The minimum of 13 founder events suggested by the ITS trees include 8 that did not result in speciation: 3 of *Dubautia plantaginea*, 3 of

D. laxa, and either 1 of *D. linearis* and 1 of *D. scabra* or 2 of *D. scabra*. Considering chromosome evolution (Carr and Kyhos, 1986), parsimony dictates that *D. scabra* is more likely to have dispersed without speciation, thus favoring two dispersals of *D. scabra* without speciation. Otherwise, two origins of the $n = 13$ genomic arrangement are indicated.

In addition, the ITS reconstructions indicate a minimum of five inter-island dispersals that led to speciation. A Kaua'i silversword alliance origin dictates at least two inter-island dispersals in *Argyroxiphium* and three in *Dubautia-Wilkesia*, whereas Maui Nui or Hawai'i origin requires at least one inter-island dispersal in *Argyroxiphium* and four in *Dubautia-Wilkesia*. In all three scenarios, no more than one founder event that led to speciation is unequivocally indicated on each island or island group in each of the two main lineages, *Argyroxiphium* and *Dubautia-Wilkesia*.

In the absence of assumptions about the history of *Argyroxiphium*, ITS analyses (see Figure 13.6) unambiguously agree with Carr et al. (1989) on several points, including (1) monophyly and North American ancestry of the silversword alliance; (2) monophyly of *Argyroxiphium*; (3) monophyly of the younger island endemic species of *Dubautia* (i.e., *Dubautia* section *Railliardia*); (4) polyphyly and, therefore, independent colonizations of *Dubautia* species on each of the islands younger than Kaua'i) (i.e., of *D. plantaginea*, *D. laxa* [on O'ahu and Maui Nui], and members of *Dubautia* section *Railliardia*); (5) Maui Nui ancestry for all Hawai'i endemics; and (6) origin of *D. herbstobatae* and *D. sherffiana* from a common immigrant to O'ahu. Assumption of a Kaua'i sister group to modern *Argyroxiphium* species (see above) results in two other points of agreement with Carr et al. (1989): (1) an original founder event of the silversword alliance ancestor on Kaua'i (pre-Kaua'i considerations aside) and (2) descent of all modern Kaua'i species from that single founder event.

ECOLOGICAL HISTORY OF THE SILVERSWORD ALLIANCE

Evolutionary diversification of the silversword alliance apparently was accompanied by major, and repeated, ecological shifts. Under the simplest formulation, with only two main habitat classes, the ITS trees suggest that diversification of the alliance included five or more evolutionary transitions between wet and dry habitats (Figure 13.7). The independent

habitat shifts reconstructed in the *Argyroxiphium* and *Dubautia* section *Railliardia* lineages are particularly striking. Although species in the two lineages differ radically in growth form and reproductive mode, they grow in sympatry or near sympatry in both wet and dry habitats on Maui Nui and Hawai'i (Robichaux et al., 1990).

Comparison of the biogeographic and ecological reconstructions (see Figures 13.6 and 13.7) suggests that major ecological shifts occurred at least once on most of the islands or island groups. Such changes occurred in the *Wilkesia gymnoxiphium*–*W. hобыi*–*Dubautia latifolia*–*D. paleata*–*D. raillardoides* lineage on Kaua'i, the *D. herbstobatae*–*D. sherffiana* lineage on O'ahu, the *D. menziesii*–*D. platyphylla*–*D. reticulata* lineage on the Maui Nui complex, and the *D. arborea*–*D. ciliolata*–*D. linearis*–*D. scabra* lineage on the Maui Nui complex or Hawai'i. The repeated occurrence of habitat shifts suggests that these changes were important in the evolution of new taxa following inter-island dispersal and colonization.

In fact, the extent of ecological shifts has been much greater than implied by the simple formulation used in the reconstructions. The diversity of habitats occupied by silversword alliance species is exceptional among Hawaiian Islands plant groups. These habitats range in elevation from 75 to 3,750 m and in annual precipitation from less than 400 to more than 12,300 mm (Robichaux et al., 1990). Among the wet habitats occupied by silversword alliance species are bogs, for example, which are characterized by poorly drained, acidic substrates and dwarfed vegetation (Canfield, 1986; Gagné and Cuddihy, 1990). Despite the harshness of the bog environment, silversword alliance taxa grow in bogs on all four islands or island groups: *Dubautia imbricata* subsp. *acronaea* G. Carr, *D. paleata*, and *D. waialealae* on Kaua'i; *D. laxa* subsp. *hirsuta* on Kaua'i and O'ahu; *Argyroxiphium caliginis* and *A. grayanum* on Maui Nui; and *A. kauense* on Hawai'i. These bog taxa belong to at least three different lineages, based on the ITS trees (see Figure 13.5), including the *Argyroxiphium* lineage and the two Kaua'i lineages within *Dubautia*–*Wilkesia* (*D. imbricata* subsp. *acronaea* and *D. waialealae* remain to be sampled for DNA-level variation). Thus, the shift to bog habitats may have occurred multiple times within the silversword alliance. More definitive resolution of the full range of ecological shifts should become possible on achievement of a more complete understanding of silversword alliance phylogeny.

SUMMARY

Multiple lines of genetic evidence, including the ITS results herein, indicate that the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, *Wilkesia*) is a monophyletic lineage derived from within *Madia-Raillardiopsis*, a primarily California FP group in subtribe Madiinae (Heliantheae). These data suggest that the silversword alliance ancestor was a self-incompatible, radiate, California FP tarweed that was externally bird-dispersed to the Hawaiian Islands, probably to Kaua'i or a pre-Kaua'i island. Based on ITS data, a minimum of only 13 inter-island dispersals could account for the modern distribution of the 28 silversword alliance species. Speciation resulted from as few as 5 of these 13 hypothetical founder events. The ITS trees also suggest that major ecological shifts between wet and dry habitats accompanied speciation on most or all islands or island groups and thus were fundamental to diversification in the silversword alliance. Enhanced phylogenetic resolution within *Argyroxiphium* and *Dubautia* and additional data on basal relationships among the major silversword alliance lineages will be crucial to an improved understanding of the biogeographic and ecological history of this fascinating group of plants.

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CCTTCTCAGAGCCTCCGTGCTGCCTGAGCTGGTGGTGTCCCTTCGCATCTCATTTTGGTACTTTGTCACTGAGTTGGGCTGATCCTCGGTGCATAATCCTCCCTTACAGCACGTTTGCT
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CCCCCTCAGAGCCTCCGTGCTTCCGTGCTGCCCTGAGCTGGCGGTGTCCCTTCGCATCTCATTTTGAACCTATTAAGTGGGTGGGTGATCCTTGGTGACAAATCCTCCTTACAGCGCGTTTGCT
CCCCCTCAGAGCCTCCGTGCTGCCCTGAGCTGGCGGTGTCCCTTCGCATCTCATTTTGAACCTATTAAGTGGGTGGGTGATCCTTGGTGACAAATCCTCCTCAGAGTACGTTTGCT
CCCCCTCAGAGCCTCCGTGCTGCCCTGAGCTGGCGGTGTCCCTTCGCATCTCATTTTGAACCTATTAAGTGGGTGGGTGATCCTTGGTGACAAATCCTCCTTACAGCGMGTTGCT

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Molecular Evolution, Adaptive Radiation, and Geographic Speciation in *Cyanea* (Campanulaceae, Lobelioideae)

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Cyanea, the largest of the seven genera of native Hawaiian lobelioids, is of considerable evolutionary interest for four reasons. First, it is the largest genus of plants endemic to the Hawaiian Islands, with 55 species comprising 5.7% of the native flora (Wagner et al., 1990; Lammers, 1992). Second, *Cyanea* and the three other lobelioid genera with fleshy fruits (*Clermontia*, *Delissea*, and *Rollandia*) are considered by many to be the largest group of Hawaiian plants to have evolved from a single immigrant, encompassing some 98 species (Rock, 1919; Carlquist, 1965, 1980; Lammers, 1990a, 1992).

Third, *Cyanea* has undergone a striking series of adaptive radiations in growth form, leaf size and shape, and floral morphology (Carlquist, 1965, 1974, 1980). *Cyanea* varies in height from 1 to 14 m and includes treelets, shrubs, trees, and even one vinelike species; most are unbranched and occur in mesic and wet forests (1,000 to 2,000 m elevation). *Cyanea* leaves vary from simple to doubly compound and range from 0.3 to 25 cm in width and up to 100 cm in length (Lammers, 1990a). Together with most Hawaiian lobelioids, *Cyanea* appears to have coevolved with honeycreepers (Drepanidinae) and honeyeaters (Meliphagidae), native birds that served as pollinators; *Cyanea* shows an unusually wide inter-specific range in corolla tube length, from 15 to 85 mm (Carlquist, 1980; Lammers and Freeman, 1986; Lammers, 1990a).

Finally, *Cyanea* shows a remarkable degree of endemism. Not only are all its species—like those of five of the other six genera of native

lobelioids—restricted to the Hawaiian archipelago, but many are endemic to single islands or portions of islands (Table 14.1), each of known geologic age (Clague and Dalrymple, 1987) and greatly isolated from the nearest areas supporting other lobelioids (Wimmer, 1943; Lammers, 1985). *Cyanea*—and the endemic Hawaiian lobelioids generally—thus provide superb material for studies of adaptive radiation and geographic speciation and for estimates of the time required for the diversification of a species-rich island clade.

We have begun an intensive study of molecular evolution in the native Hawaiian lobelioids, with a focus on *Cyanea* and related genera with fleshy, bird-dispersed fruits. Our aim is to derive a phylogeny based on restriction site variation in chloroplast DNA (cpDNA) and to use this independently derived phylogeny as a basis for interpreting patterns of adaptive radiation and geographic speciation. An independently derived phylogeny is particularly crucial for studies of adaptive radiation. Although adaptive radiation is probably the most important concept bridging ecology and evolutionary biology, very few cases have been rigorously analyzed (Givnish, 1987; Skinner, 1988; Carr et al., 1989; Baldwin et al., 1990, 1991; Sytsma et al., 1991). The fundamental problem is that, in almost every case, the very characters whose radiation is being studied (e.g., beak size and shape) are also used to classify the organisms in question, so that the exercise can become circular, chasing morphological traits down evolutionary pathways determined, at least in part, by the traits themselves.

Many studies have demonstrated that variation in cpDNA restriction sites can provide a powerful tool for inferring relationships among plant species, genera, and even families (e.g., Sytsma and Gottlieb, 1986; Jansen and Palmer, 1987, 1988; Palmer et al., 1988; Wendel, 1989; Baldwin et al., 1990; Olmstead et al., 1990, 1992; Sytsma, 1990; Baldwin, 1992; Downie and Palmer, 1992a; Doyle et al., 1992; Jansen et al., 1992; Sytsma and Smith, 1992; Wendel and Albert, 1992). Analyses based on cpDNA restriction site variation show significantly less homoplasy (convergence or parallelism, likely to distort inferences of phylogeny) than do those based on morphology (Givnish and Sytsma, 1992; contra Sanderson and Donoghue, 1989, and Donoghue and Sanderson, 1992). The large number of independent characters sampled in cpDNA analyses, their low level of homoplasy for a given number of taxa, and the conserved architecture of the chloroplast genome ensure that restriction sites can provide detailed and precise data on phylogenetic relationships

TABLE 14.1. Distribution of Species of *Cyanea* and Related Lobelioids in the Hawaiian Archipelago

| Species | Kaua'i | W O'ahu | E O'ahu | Moloka'i | Lana'i | W Maui | E Maui | Hawai'i |
|--|--------|---------|---------|----------|--------|--------|--------|---------|
| <i>Cyanea aculeatiflora</i> Rock | | | | | | | • | |
| <i>C. acuminata</i> (Gaud.) Hillebr. | | • | | | | | | |
| <i>C. angustifolia</i> (Cham.) Hillebr. | | • | • | • | • | • | | |
| <i>C. arborea</i> Hillebr. | | | | | | | † | |
| <i>C. asarifolia</i> St. John | V | | | | | | | |
| <i>C. asplenifolia</i> (H. Mann) Hillebr. | | | | | | † | | |
| <i>C. comata</i> Hillebr. | | | | | | | † | |
| <i>C. copelandii</i> Rock | | | | | | | • | † |
| <i>C. coriacea</i> (A. Gray) Hillebr. | • | | | | | | | |
| <i>C. degeneriana</i> E. Wimm. | | | | | | | | • |
| <i>C. dunbarii</i> Rock | | | | V | | | | |
| <i>C. eleeleensis</i> (St. John) Lammers | V | | | | | | | |
| <i>C. elliptica</i> (Rock) Lammers | | | | | • | • | • | |
| <i>C. fauriei</i> H. Lév. | • | | | | | | | |
| <i>C. fissa</i> (H. Mann) Hillebr. | • | | | | | | | |
| <i>C. giffardii</i> Rock | | | | | | | | † |
| <i>C. glabra</i> (E. Wimm.) St. John | | | | | | | • | |
| <i>C. grimesiana</i> Gaud. | | • | • | • | • | | | † |
| <i>C. hamatiflora</i> Rock | | | | | | | • | V |
| <i>C. hardyi</i> Rock | • | | | | | | | |
| <i>C. hirtella</i> (H. Mann) Hillebr. | • | | | | | | | |
| <i>C. horrida</i> (Rock) Degener & Hosaka | | | | | | | • | |
| (Continued) | | | | | | | | |

Notes: Extant populations are indicated by •; endangered populations by V; extinct populations by †; and possible, but not definitely documented, occurrence by ?.

TABLE 14.1. (Continued)

| Species | Kaua'i | W O'ahu | E O'ahu | Moloka'i | Lana'i | W Maui | E Maui | Hawai'i |
|--|--------|---------|---------|----------|--------|--------|--------|---------|
| <i>Cyanea kolekolensis</i> (St. John) Lammers | V | | | | | | | |
| <i>C. kunthiana</i> Hillebr. | | | | | | • | • | |
| <i>C. leptostegia</i> A. Gray | • | | | | | | | |
| <i>C. linearifolia</i> Rock | V | | | | | | | |
| <i>C. lobata</i> H. Mann | | | | | † | † | | |
| <i>C. longissima</i> (Rock) St. John | | | | | | | † | |
| <i>C. macrostegia</i> Hillebr. | | | | | • | • | • | |
| <i>C. mannii</i> (Brigham) Hillebr. | | | | • | | | | |
| <i>C. marksii</i> Rock | | | | | | | | V |
| <i>C. mceldowneyi</i> Rock | | | | | | | V | |
| <i>C. membranacea</i> Rock | | • | | | | | | |
| <i>C. obtusa</i> (A. Gray) Hillebr. | | | | | | † | † | |
| <i>C. pilosa</i> A. Gray | | | | | | | | • |
| <i>C. pinnatifida</i> (Cham.) E. Wimm. | | † | V | | | | | |
| <i>C. platyphylla</i> (A. Gray) Hillebr. | | | | | | | | V |
| <i>C. pohaku</i> Lammers | | | | | | | † | |
| <i>C. procera</i> Hillebr. | | | | V | | | | |
| <i>C. profuga</i> C. Forbes | | | | † | | | | |
| <i>C. pycnocarpa</i> (Hillebr.) E. Wimm. | | | | | | | | † |
| <i>C. quercifolia</i> (Hillebr.) E. Wimm. | | | | | | | † | |
| <i>C. recta</i> (Wawra) Hillebr. | V | | | | | | | |
| <i>C. remyi</i> Rock | V | | | | | | | |
| <i>C. scabra</i> Hillebr. | | | | | | • | | |
| <i>C. shipmanii</i> Rock | | | | | | | | † |
| <i>C. solanacea</i> Hillebr. | | | | • | | ? | | |
| <i>C. solenocalyx</i> Hillebr. | | | | V | | | | |
| <i>C. spathulata</i> (Hillebr.) A. Heller | • | | | | | | | |
| <i>C. stictophylla</i> Rock | | | | | | | | V |

(Continued)

TABLE 14.1. (Continued)

| Species | Kaua'i | W O'ahu | E O'ahu | Moloka'i | Lana'i | W Maui | E Maui | Hawai'i |
|---|--------|---------|---------|----------|--------|--------|--------|---------|
| <i>Cyanea superba</i> (Cham.) A. Gray | | † | V | | | | | |
| <i>C. sylvestris</i> A. Heller | • | | | | | | | |
| <i>C. tritomantha</i> A. Gray | | | | | | | | • |
| <i>C. truncata</i> (Rock) Rock | | V | | | | | | |
| <i>C. undulata</i> C. Forbes | V | | | | | | | |
| <i>Clermontia arborescens</i> (H. Mann) Hillebr. | | | | • | • | • | • | |
| <i>C. calophylla</i> E. Wimm. | | | | | | | | • |
| <i>C. clermontioides</i> (Gaud.) A. Heller | | | | | | | • | |
| <i>C. drepanomorpha</i> Rock | | | | | | | • | |
| <i>C. fauriei</i> H. Lév. | • | • | • | | | | | |
| <i>C. grandiflora</i> Gaud. | | | | • | • | • | • | |
| <i>C. hawaiiensis</i> (Hillebr.) Rock | | | | | | | | • |
| <i>C. kakeana</i> Meyen | | • | • | • | | • | • | |
| <i>C. kohalae</i> Rock | | | | | | | | • |
| <i>C. lindseyana</i> Rock | | | | | | | • | † |
| <i>C. micrantha</i> (Hillebr.) Rock | | | | | † | • | | |
| <i>C. montis-loa</i> Rock | | | | | | | | • |
| <i>C. multiflora</i> Hillebr. | | † | | | | † | | |
| <i>C. oblongifolia</i> Gaud. | | • | • | • | † | • | † | |
| <i>C. pallida</i> Hillebr. | | | | • | | | | |
| <i>C. parviflora</i> Gaud. ex A. Gray | | | | | | | | • |
| <i>C. peleana</i> Rock | | | | | | | † | V |
| <i>C. persicifolia</i> Gaud. | | • | • | | | | | |
| <i>C. pyrularia</i> Hillebr. | | | | | | | | V |
| <i>C. samuelii</i> C. Forbes | | | | | | | • | |
| <i>C. tuberculata</i> C. Forbes | | | | | | | V | |
| <i>C. waimeae</i> Rock | | | | | | | | • |
| <i>Delissea fallax</i> Hillebr. | | | | | | | | † |
| <i>D. laciniata</i> Hillebr. | | | † | | | | | |
| <i>D. lauliiana</i> Lammers | | | † | | | | | |

(Continued)

TABLE 14.1. (Continued)

| Species | Kaua'i | W O'ahu | E O'ahu | Moloka'i | Lana'i | W Maui | E Maui | Hawai'i |
|--|--------|---------|---------|----------|--------|--------|--------|---------|
| <i>Delissea parviflora</i> Hillebr. | | | | | | | | † |
| <i>D. rhytidosperma</i> H. Mann | V | | | | | | | |
| <i>D. rivularis</i> (Rock) E. Wimm. | V | | | | | | | |
| <i>D. sinuata</i> Hillebr. | | † | | | † | | | |
| <i>D. subcordata</i> Gaud. | | • | † | | | | | |
| <i>D. undulata</i> Gaud. | † | † | | | | † | | V |
| <i>Rollandia angustifolia</i> (Hillebr.) Rock | | | • | | | | | |
| <i>R. crispa</i> Gaud. | | | • | | | | | |
| <i>R. humboldtiana</i> Gaud. | | • | | | | | | |
| <i>R. lanceolata</i> Gaud. | | • | • | | | | | |
| <i>R. longiflora</i> Wawra | | • | • | | | | | |
| <i>R. parvifolia</i> C. Forbes | † | | | | | | | |
| <i>R. purpurellifolia</i> Rock | | † | | | | | | |
| <i>R. st.-johnii</i> Hosaka | | | • | | | | | |
| <i>Brighamia insignis</i> A. Gray | • | | | | | | | |
| <i>B. rockii</i> St. John | | | | • | † | | | |

Sources: Data compiled from Rock (1919); Lammers (1990a, 1992); personal communications with L. Cuddihy, R. Hobdy, J. Obata, and L. Mehroff; and personal observations of the authors.

(Palmer and Stein, 1986; Palmer et al., 1988; Clegg et al., 1990; Sytsma, 1990).

Attention must be paid to instances in which the chloroplast genome is involved as a single genetic unit in hybridization or introgression events (see Rieseberg and Brunsfeld, 1992) or in which the chloroplast genome exhibits rearrangements (Downie and Palmer, 1992b). The first is probably not an issue, as reports of hybridization in *Cyanea* are rare (Rock, 1919; Lammers, 1990a). The latter is of some concern, as some Lobelioideae show several nested rearrangements of the chloroplast genome (Knox et al., 1993). However, these rearrangements have been

precisely mapped relative to the small *Nicotiana* cpDNA probes that were used in this study (see below), thus permitting unambiguous interpretation of restriction fragment patterns. Any analysis based on cpDNA variation must consider the possibility that sorting of maternal plastid lineages from a polymorphic ancestor (Neigel and Avise, 1986) might lead to a phylogeny at odds with the actual phylogeny. Lineage sorting, however, seems unlikely to be important in Hawaiian plant groups, given the small population sizes and frequent genetic bottlenecks associated with the repeated colonization of new islands.

This chapter presents a progress report on our studies of cpDNA evolution, adaptive radiation, and speciation in *Cyanea*. First, we summarize the natural history of *Cyanea* and the other fleshy-fruited genera. We then present the results of a preliminary analysis of relationships among the fleshy-fruited genera and 24 of the 45 extant species of *Cyanea* and explore their evolutionary implications. Finally, we discuss the factors that may have caused greater speciation and greater exposure to extinction in *Cyanea* than in the closely related genus *Clermontia*, and the consequent need for a vigorous program to preserve the remaining, often highly endangered species of *Cyanea*.

NATURAL HISTORY OF THE FLESHY-FRUITED HAWAIIAN LOBELIOIDS

Among the four fleshy-fruited (baccate) genera, *Cyanea* is by far the most species-rich and diverse in habit (Table 14.1). Species of *Cyanea* are generally unbranched trees or treelets of mesic and wet forest interiors (Figure 14.1A to E). A few species (e.g., *C. coriacea*, *C. hardyi*) are sparsely branched shrubs of forest openings and edges, often in areas with lower rainfall (Rock, 1919); one (*C. copelandii*) is vinelike. *Cyanea* flowers are tubular, often strongly curved, and white to purple in color (occasionally pink, yellow, or greenish); their floral tube is cut only about halfway to the base (Figure 14.1B). *Cyanea* fruits are orange or purplish in color and generally less than 15 mm in diameter. Species differ dramatically in stature. For example, *C. degeneriana* (found in wet forests on Hawai'i) is a subherbaceous treelet usually less than 1 m tall (Figure 14.1A); *C. mceldowneyi* of Maui grows up to 2 m (Figure 14.1C); *C. tritomantha* of Hawai'i is taller still, with a massive trunk and palmlike growth form, up to 3 m (Figure 14.1D); and a few gigantic species, such as *C. hamatiflora* of Maui and Hawai'i or *C. leptostegia* of Kaua'i, can achieve heights up to 14 m (Figure 14.1E).

Leaves of different *Cyanea* species can differ dramatically in size, from 3 mm wide in *C. linearifolia* to more than 25 cm wide and up to 1 m in length in some of the palmlike species (e.g., *C. aculeatiflora*, *C. hamatiflora*, *C. leptostegia*, and *C. macrostegia*) (Rock, 1919; Carlquist, 1965, 1980; Lammers, 1990a). Although most species have leaves with entire or minutely toothed margins, some are coarsely toothed, lobed, deeply divided, or pinnately compound (Figure 14.2). One species (*C. shipmanii* of Hawai'i) even has doubly pinnately compound leaves that resemble those of tree ferns. Most species with undivided leaves have tapered or rounded leaf bases, but one cliff-dwelling species (*C. asarifolia* of Kaua'i) has leaves with cordate bases, like those of many bole-climbing vines with erect petioles and horizontal leaves (Givnish and Vermeij, 1976; Givnish, 1986). Most species with nonentire leaf margins show marked differences between juvenile and adult leaves, with the juvenile foliage being more deeply divided (Figures 14.2 and 14.3) (Carlquist, 1965, 1974, 1980; Lammers, 1990a,b).

The juvenile foliage or stems of some species are also armed with thornlike prickles (conical outgrowths of ground tissue) (Carlquist, 1962), up to 1 cm in length (Figure 14.4). Given the absence of native terrestrial mammals and reptiles that could browse or graze vegetation near the ground, what is the significance of such prickles? Carlquist (1962, 1965, 1974, 1980) suggested that they may have defended lobelioids against herbivory by native tree snails (Succinidae). This seems unlikely, however, given that these snails have never been observed to consume lobelioid leaves and, like achatinellid snails (the largest group of terrestrial mollusks native to the Hawaiian Islands), usually graze instead on fungi (especially epiphyllid fungi) (Henshaw, 1912–14; Carlquist, 1974; S. Carlquist, unpubl.; M. G. Hadfield, unpubl.).

Givnish et al. (1994) proposed an alternative explanation: Prickles near ground level protected *Cyanea* stems and leaves from browsing by large native terrestrial birds, the eight species of large flightless geese and gooselike moa-nalos (derived from mallardlike ducks), which were extirpated by the Polynesians sometime in the past 1,600 years (Olson and James, 1982a). Subfossil remains of these large browsers have recently been discovered in lava tubes and calcified sand dunes (Olson and James, 1982b, 1991). *Cyanea* may have been particularly sensitive to damage by these browsers, given its unbranched habit and its tender, poorly defended foliage and stems that pigs and goats avidly eat today (Loope and Scowcroft, 1985; L. Cuddihy et al., unpubl.). Several groups of birds (e.g., moas on New Zealand, elephant birds on Madagascar, *Sylviornis* on

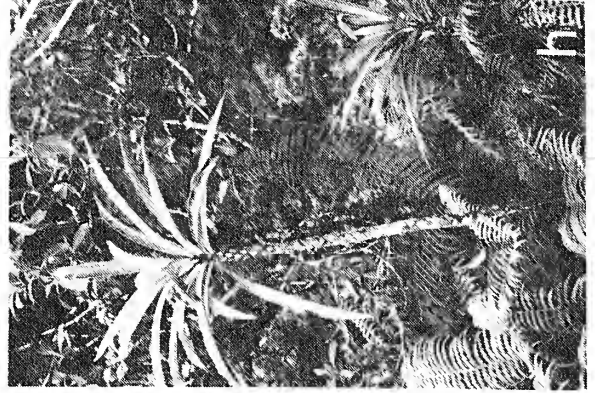
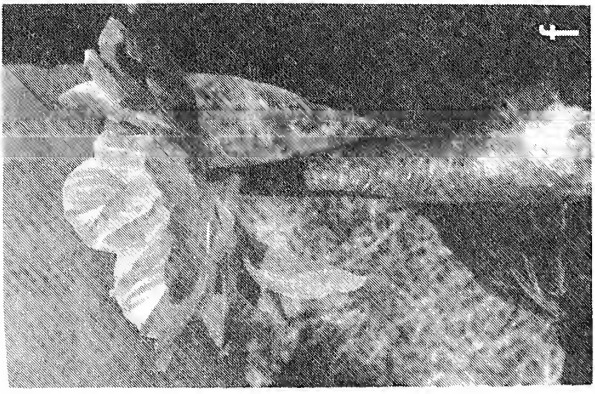
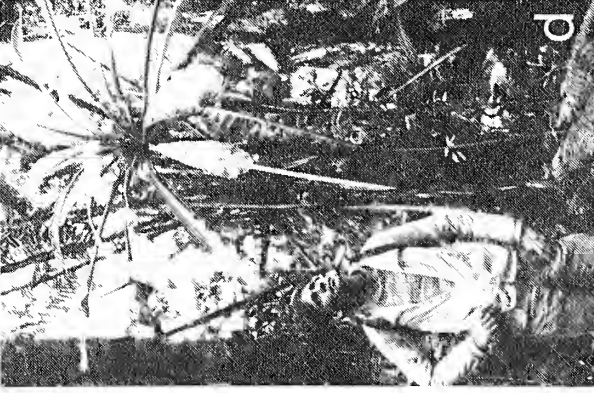
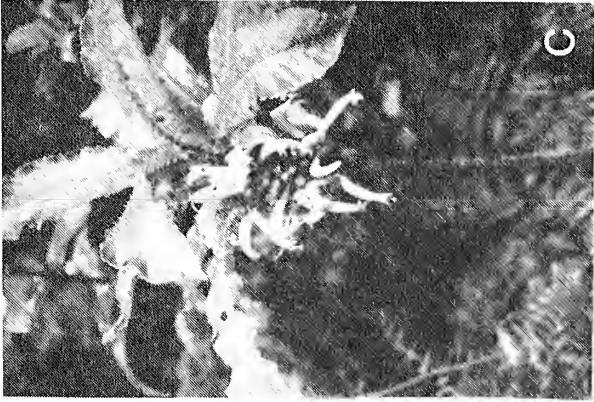


FIGURE 14.1.1. Habit of representative species of *Cyanea* and allied genera. (a and b) *C. degeneriana*, 'Ola'a Forest Reserve, Hawai'i, ca. 0.8 m tall: (a) habit; (b) close-up of flowers (ca. 20 mm long) and orange fruits. (c) *C. mceldowneyi*, Waikamoi stream area, Maui, ca. 1 m tall. (d) *C. tritomantha*, Desolation Trail, Hawai'i, with K. J. Sytsma. (e) *C. hamatiflora* (emergent rosette tree with narrow leaves on far side of stream near middle of photograph; note human figures in stream for scale), Waikamoi Flume, Maui. (f) *Brighamia insignis*, Kaua'i (from Carlquist, 1980; reproduced courtesy of the National Tropical Botanical Garden). (g) *Clermontia kakeana*, 'Iao Valley, Maui, with R. Hobby. (h) *Rollandia angustifolia*, O'ahu. (i) *Delissea undulata*, Hawai'i (from Rock, 1919; reproduced courtesy of Bishop Museum Press, Bishop Museum, Honolulu, Hawaii).

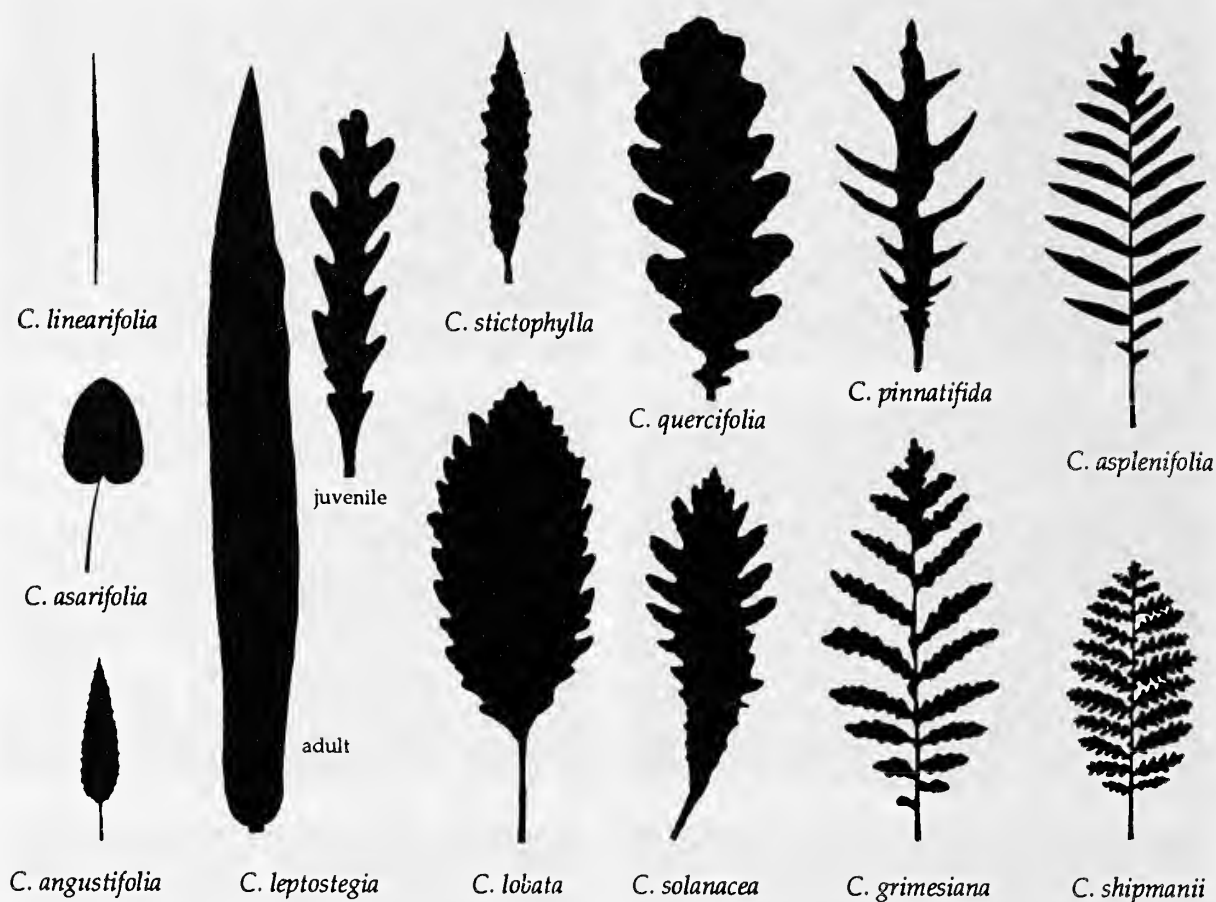


FIGURE 14.2. Interspecific variation in leaf size and shape within *Cyanea* (redrawn from Carlquist, 1965; Lammers, 1990b; and authors' photographs).

New Caledonia, and possibly dodos, solitaires, or rails on the Mascarene Islands) have been able to disperse to oceanic islands inaccessible to nonflying mammals, where they then evolved into terrestrial (and often flightless) browsers and grazers, the insular equivalents of antelopes or cervids (Carlquist, 1965; Balouet, 1984; Balouet and Olson, 1989; Olson and James, 1991). Although prickles are rare in floras of such bird-dominated islands, the densely divaricate branching patterns of the juveniles of several New Zealand trees (55 species in 21 families) apparently played a similar role as a mechanical defense against browsing by moas (Carlquist, 1974; Atkinson and Greenwood, 1989).

The corollas of *Cyanea* differ dramatically in length (15 to 80 mm) and coloration (Figure 14.5). The average corolla length of species on Kaua'i is significantly less than that on younger islands (Figure 14.6), perhaps reflecting an escalating evolutionary competition for progressively more specialized pollinators. As noted by Rock (1919) and others, the strong curvature of the flowers of most *Cyanea* (and other lobelioids except *Brighamia*) is strongly reminiscent of the curved bills of the 'Iwi (*Vestiaria coccinea*) and other nectarivorous honeycreepers. Research by

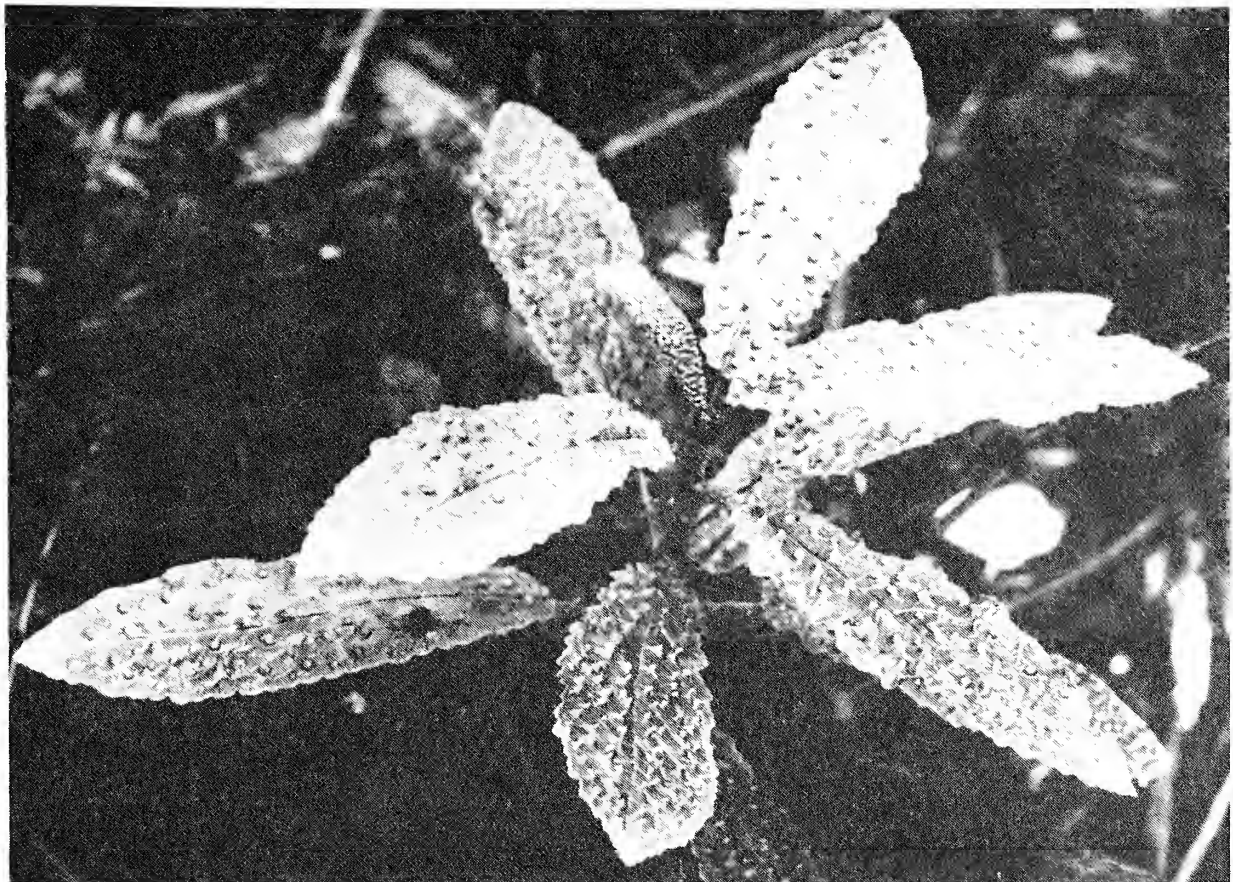
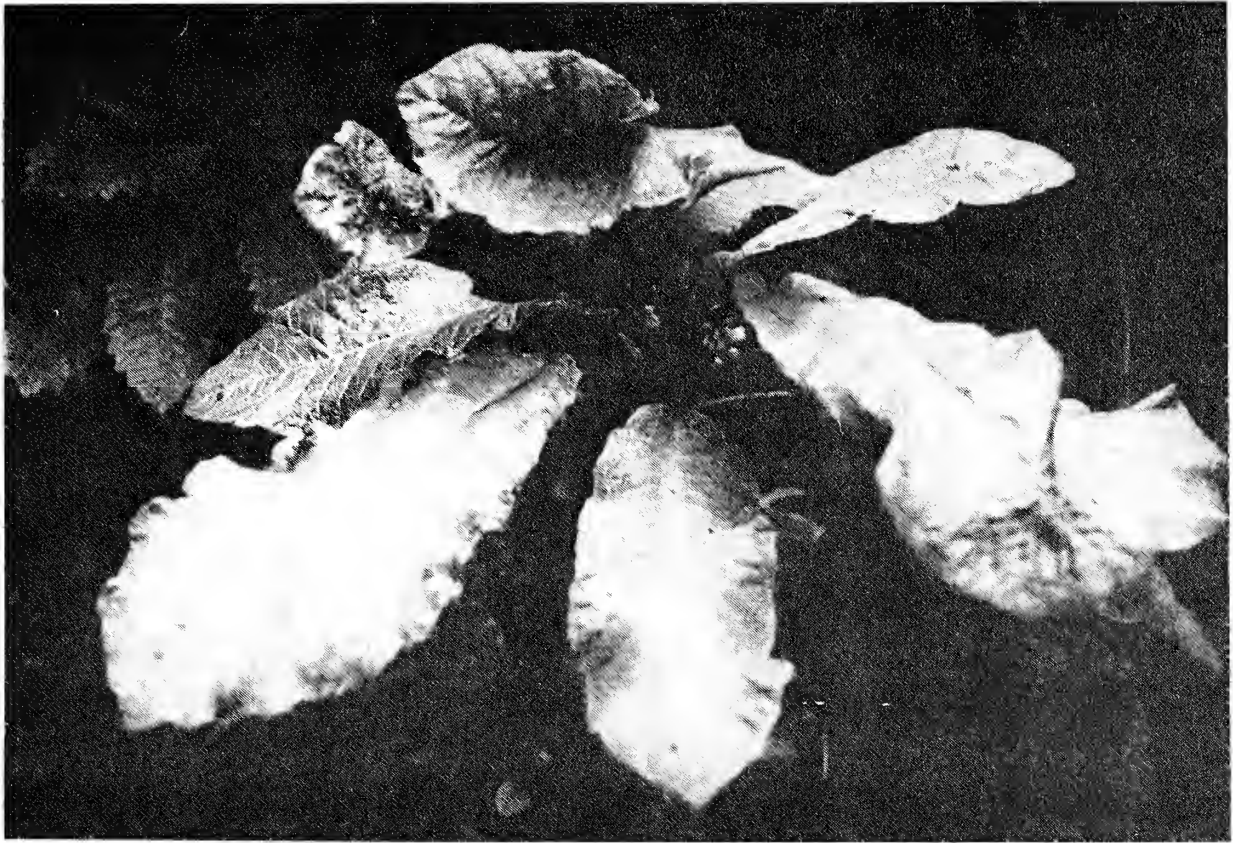


FIGURE 14.3. Examples of juvenile–adult leaf dimorphism in *Cyanea*. (Above) *C. solenocalyx* (Kamakou Reserve, The Nature Conservancy, Moloka‘i), with dentate, nearly orbiculate juvenile leaves in shadows at upper left, adult leaves below and to right. (Below) *C. tritomantha* seedling, showing thornlike prickles scattered over leaf surfaces (see smooth adult foliage in Figure 14.1D).



FIGURE 14.4. Juvenile shoots of *Cyanea solanacea* on Moloka'i (Kamakou Reserve), showing dense aggregation of thornlike prickles (ca. 1 cm in length) and deeply lobed juvenile foliage. These shoots are sprouts from an adult axis (visible at the bottom of the photograph) that had been mechanically damaged by feral pigs, a recently introduced alien herbivore. Note the loss of prickles toward the tip of the juvenile shoots, signaling the beginning of the shift toward adult morphology.

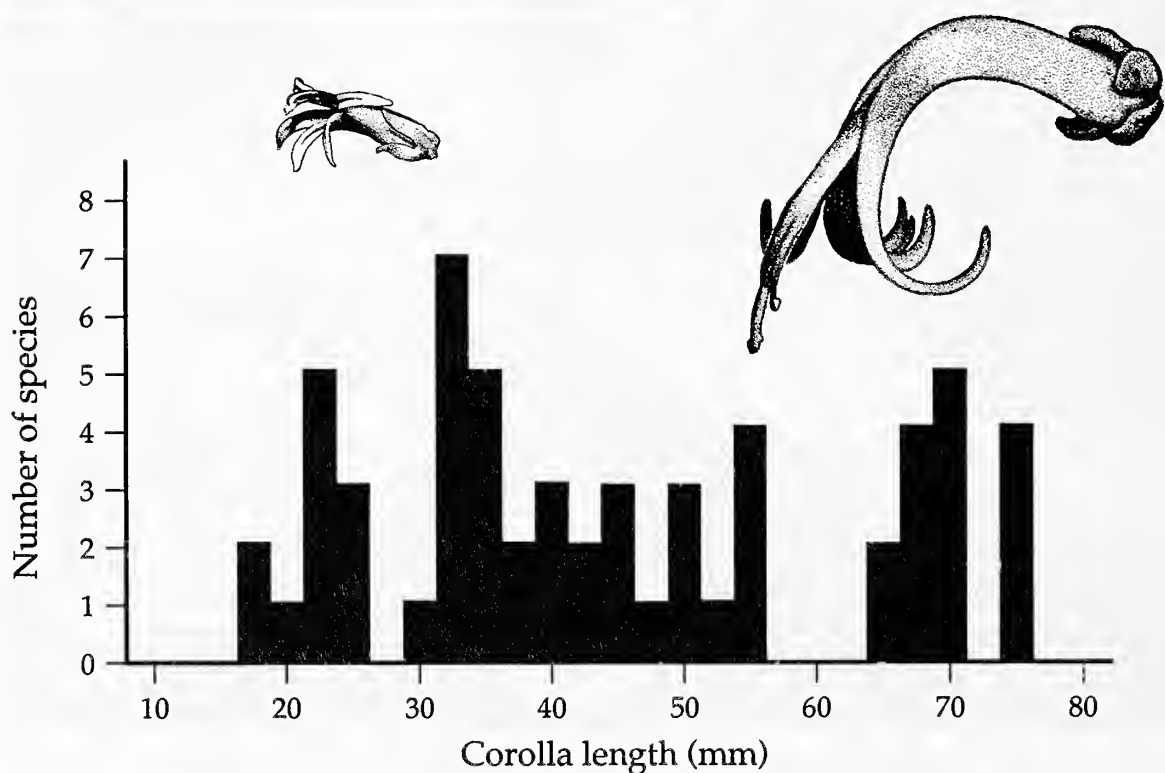
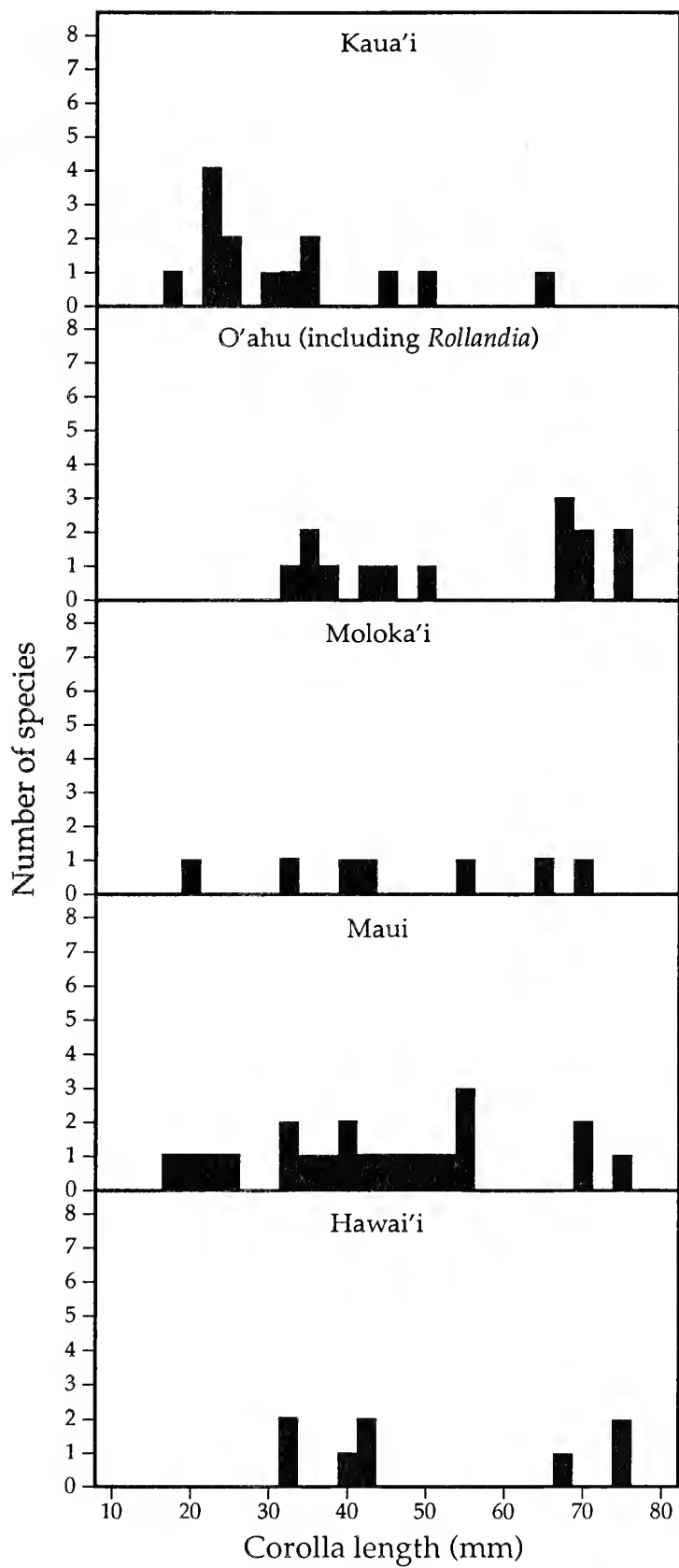


FIGURE 14.5. Interspecific variation in typical corolla tube length in *Cyanea* and *Rollandia*; values are means of maximum and minimum lengths reported by Lammers (1990a). Representative flowers shown are those of *C. fissa* from Kaua'i (left) and *C. superba* from O'ahu.

FIGURE 14.6. Distribution of corolla tube lengths in species of *Cyanea* and *Rollandia* native to each of the six high islands in the Hawaiian archipelago. The average length of corollas on Kaua'i is significantly less ($P < .05$; two-tailed t tests) than that seen on the other islands.



Lammers and Freeman (1986) revealed that most lobelioids have a nectar sugar profile typical for bird pollination, except *Brighamia* (see Figure 14.1F), which seems likely to be pollinated by hawk moths.

Clermontia, with 22 species, is the second largest Hawaiian genus of lobelioids. It differs from *Cyanea* in having reduced inflorescences, possessing a repeatedly branched, shrubby habit (see Figure 14.1G), and

occurring mainly in forest edges and gaps rather than shaded understories. A few species (mainly on Hawai'i) are epiphytic. The orange fruits of *Clermontia* are unusually large, 20 to 40 mm in diameter, larger than those typical of all other fleshy-fruited lobelioid genera; the pericarp (rind) is also unusually thick. The flowers are cleft all the way to the base of the corolla, suggesting that they may have excluded fewer potential pollinators than flowers of comparable size in *Cyanea*. Flowers range from less than 20 mm long in some species (e.g., *Clermontia parviflora*) to 80 mm long in others (e.g., *C. grandiflora*). Flower colors are generally pink, greenish, or whitish, but several species on Hawai'i have spectacular, wine-red corollas (e.g., *C. drepanomorpha*). In the latter and most other species of *Clermontia*, the sepals resemble the petals, giving the flowers a "doubled" appearance.

Rollandia is a small genus (six extant species, two extinct) of treelets now restricted to O'ahu, generally found in the understory of mesic to wet forests at middle elevations (see Figure 14.1H). The flowers are similar to those of *Cyanea*, but have the staminal column fused to the corolla (Lammers, 1990a). One extraordinary species (*R. st.-johnii*) is a compact, prickly treelet hugging some of the most remote and wind-swept ridges of east O'ahu.

Finally, *Delissea* is a relictual genus, of which only four of nine species now survive. It has an unusual growth form, with a rather narrow crown atop a tall, slender stem (see Figure 14.1I). *Delissea* species apparently occurred in rather open dry forest as well as mesic forest (Rock, 1919). The flowers differ from *Cyanea* in having one or more knoblike projections on the corolla.

Clermontia, *Cyanea*, *Delissea*, and *Rollandia* share fleshy fruits, axillary inflorescences, and a woody habit, an unusual combination among lobelioids worldwide. This has led many authors to conclude that the group is monophyletic. The most widely held view (advanced by Rock, 1919) is that their closest relative is either *Centropogon* or *Burmeistera*, both shrubs with fleshy fruits from cloud forests in Central and South America. However, Lammers (1985) proposed that certain woody species of *Pratia* section *Collensoa* from Borneo, with fleshy fruits and axillary inflorescences, may be more closely related.

With regard to the three capsular genera of Hawaiian lobelioids, Rock (1919) suggested that the closest relative of *Brighamia* may be *Sclerotheca* or *Apetahia*, two closely related genera of shrubs with capsular fruits from Tahiti, or possibly the herbaceous genus *Isotoma* from Australia. One to three additional colonization events have been pro-

posed to account for the origin of *Trematolobelia* and the two Hawaiian sections of *Lobelia* (Rock, 1919; Skottsberg, 1928; Wimmer, 1943; Mabberley, 1974, 1975; Lammers, 1990a). Mabberley (1975) suggested that *Trematolobelia* may have been derived from the endemic Hawaiian *Lobelia* section *Galeatella* and that both are closely related to East Asian, Brazilian, or East African species of *Lobelia*.

MOLECULAR EVOLUTION AND PHYLOGENETIC RELATIONSHIPS

Methods and Taxa Studied

To date, we have surveyed cpDNA restriction site variation in 76 species using nine enzymes, examining all extant Hawaiian species of *Brighamia*, *Lobelia*, *Rollandia*, and *Trematolobelia*; 19 of 21 extant species of *Clermontia*; 2 of 4 extant species of *Delissea*; and 24 representative species of *Cyanea*. The latter group was chosen to sample variation within *Cyanea*, including 44% of all species (59% of extant species) and at least three species of each section recognized by Rock (1919). Our cladistic analysis used global parsimony (Maddison et al., 1984) using PAUP version 3.0s (Swofford, 1991), with outgroups consisting of representative species of *Burmeistera* and *Centropogon* from South America; *Pratia borneensis* Hemsl. from Borneo; *Sclerotheca jayorum* Raynal from Tahiti, and *Lobelia giberroa* Hemsl. from the East African highlands.

Total DNA was extracted from fresh and -80°C frozen leaf tissue, using either a modified cetyltrimethylammonium bromide (CTAB) procedure or CTAB applied to an organellar extract (Smith et al., 1991). DNA was cleaved using nine restriction endonucleases (*Bam*H I, *Bcl* I, *Bgl* II, *Cla* I, *Dra* I, *Eco*R I, *Nci* I, *Xba* I, *Xmn* I) known to generate sites with a high rate of divergence among closely related taxa. Cleaved DNA was size-separated by electrophoresis on agarose gels, transferred to nylon filters, and probed with heterologous cpDNA clones to recognize restriction site variation through comparisons of autoradiograms using standard procedures (Sytsma and Smith, 1988). To ensure colinearity of autologous and heterologous cpDNA, we used small mapped *Nicotiana* cpDNA clones (kindly supplied by S. Downie and R. Palmer), using combinations (Table 14.2) designed to take into account the cpDNA inversions mapped in Hawaiian lobelioids and our outgroups by Knox et al. (1993).

TABLE 14.2. Coordinates (modified from Knox et al., 1993) of *Nicotiana* cpDNA Clone Combinations Used to Probe Total DNAs of Hawaiian Lobelioids

| Probe | Coordinates (kb) | | | Region |
|-------|------------------|---|-------|--------------------------|
| 1 | 86.1 | → | 74.2 | Large single-copy region |
| 2 | 74.2 | → | 60.9 | Large single-copy region |
| 3 | 53.6 | → | 43.4 | Large single-copy region |
| 4 | 43.4 | → | 31.9 | Large single-copy region |
| 5 | 31.9 | → | 21.9 | Large single-copy region |
| 6 | 21.9 | → | 12.3 | Large single-copy region |
| 7 | 12.3 | → | 2.8 | Large single-copy region |
| 8 | 53.6 | → | 60.7 | Large single-copy region |
| 9 | 111.9 | → | 118.6 | Small single-copy region |
| 10 | 118.6 | → | 130.6 | Small single-copy region |

We have now analyzed restriction site variation within the large and small single-copy regions of the chloroplast genome for the 76 species mentioned above and have begun analysis of an additional 21 species of *Cyanea*. Excluding the latter, we have detected 331 mutations thus far, of which 206 are phylogenetically informative. A complete analysis of the origins and relationships of the Hawaiian lobelioids based on this data set will be published elsewhere. Here, we will outline two results crucial to understanding adaptive radiation and speciation within *Cyanea*: monophyly and relationships of the baccate genera of Hawaiian lobelioids and relationships among the species of *Cyanea*.

Phylogeny of the Baccate Hawaiian Lobelioids

Cladistic analysis identified the baccate lobelioids as a monophyletic group, with the unexpected inclusion of the cliff succulent *Brighamia* (Figure 14.7). The cladogram shown does not incorporate the large amount of genetic variation detected within *Cyanea*, represented for the moment by a single species. This has ramifications for the position of *Rollandia* (see below), but otherwise, Figure 14.7 is fully reflective of the relationships seen among all baccate species surveyed.

One of our most surprising results is that the closest relative of *Brighamia* is *Delissea*, a genus often considered on morphological grounds to have diverged from the common ancestor of the remaining baccate genera at an early date (Rock, 1919). The association of *Brighamia* with *Delissea*—strongly supported by our molecular data—may

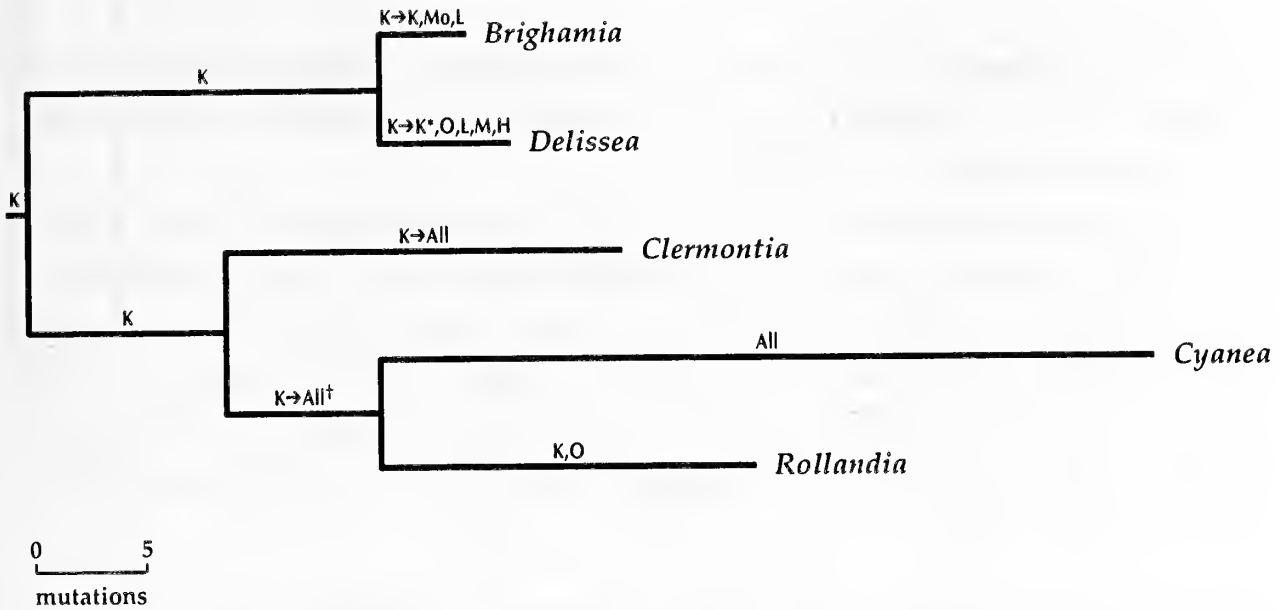


FIGURE 14.7. Phylogram showing cladistic relationships among the fleshy-fruited Hawaiian lobelioids (including *Brighamia*), based on cpDNA restriction site variation. Horizontal length of each branch is proportional to the number of mutations between taxa and inferred ancestors. Abbreviations refer to actual island distributions of current taxa and inferred island distributions of ancestral taxa (K, Kaua‘i; O, O‘ahu; L, Lana‘i; Mo, Moloka‘i; H, Hawai‘i; M, Maui). Basal condition (*) for *Delissea* was inferred from distribution of subgenera; ancestral condition for *Cyanea*-*Rollandia* (†) was taken as *Cyanea*’s current condition, given that *Rollandia* is embedded within it (see Figure 14.8). The clade shown is a complete monophyletic sublineage from a broader analysis including *Burmeistera*, *Centropogon*, *Lobelia giberroa*, *Pratia*, and *Sclerotheca* as outgroups, and *Lobelia niihauensis*, *L. gloria-montis*, and *Trematolobelia macrostachys* as additional ingroups (see text). The consistency index for the broader analysis is 0.950 (0.833 excluding autapomorphies); PAUP version 3.0s identified a single most-parsimonious tree using the branch-and-bound search strategy and DELTRAN option.

not be so surprising, at least in hindsight: They are the only Hawaiian lobelioids that share large (ca. 1.5 mm) whitish seeds and have curiously narrow crowns for their height (see Figure 14.1F and I). In retrospect, the association of *Brighamia* with the fleshy-fruited genera may also not be that surprising; it too has axillary inflorescences and fruits that are quite fleshy early in development (Lammers, 1989) but that eventually develop into dry capsules, suggesting that *Brighamia* first gained and then secondarily lost fleshy fruits during evolution. These shared morphological characters strengthen the molecular conclusion, supported by only one cpDNA mutation, that *Brighamia*-*Delissea* is the sister group to the *Clermontia*-*Cyanea*-*Rollandia* clade and that their common ancestor diverged from the common ancestor of *Clermontia*, *Cyanea*, and *Rollandia* before the latter diverged from each other. Clearly, the decision by St.

John and Takeuchi (1987) and St. John (1987) to merge *Delissea* with *Cyanea* while retaining *Clermontia* and *Rollandia* cannot be justified on molecular grounds.

Clermontia is the sister group to *Cyanea-Rollandia* (Figure 14.7). This arrangement accords with the traditional view, based on comparative morphology, that *Rollandia* is closely related to *Cyanea* and that *Clermontia* is more distantly related (Rock, 1919; Carlquist, 1965; Lammers, 1991; see also Lammers, this volume, Chapter 15). The monophyly of the *Clermontia-Cyanea-Rollandia* clade is strongly supported by the molecular data.

Evolutionary Relationships within *Cyanea*

Within *Cyanea*, cpDNA restriction site variation among extant species is greater than that seen in any of the other Hawaiian lobelioid genera or endemic sections of *Lobelia*. Using *Brighamia insignis* and *Clermontia arborescens* as outgroups, we conducted a cladistic analysis of *Cyanea* and *Rollandia* (see Table 14.3 for voucher data). One hundred fifty variable restriction sites in this group were detected, of which 78 were phylogenetically informative (Appendix 14.1). A single most-parsimonious tree was identified using PAUP version 3.0s, with the heuristic search strategy and ACCTRAN optimization option (Figure 14.8).

Cyanea divides naturally into two clades, each defined by several synapomorphies; both are well supported by the cpDNA data, based on bootstrap and decay analyses (Figure 14.8). *Rollandia* is imbedded within the first clade. It has therefore been taxonomically submerged into *Cyanea* (Lammers et al., 1993), making it the largest angiosperm genus in the Hawaiian archipelago, with 63 species. *Rollandia* is the sister group to *C. acuminata* and *C. grimesiana* from O'ahu, suggesting an origin for *Rollandia* on O'ahu (to which all species of *Rollandia* are endemic, except the extinct *R. parvifolia* from Kaua'i). Insofar as our analysis supports an earlier origin of *Clermontia* than of *Rollandia* (see Figure 14.7), it implies either that both genera have evolved recently, if one accepts the theory of an origin for *Clermontia* on Hawai'i (Lammers, 1991; see also Lammers, this volume, Chapter 15), or that *Clermontia* arose on a now submerged or eroded island considerably older than Kaua'i and that differential dispersal, speciation, and extinction has led to its greater diversity today on Maui and Hawai'i (see further discussion below).

What is the systematic significance of our cpDNA restriction site phylogeny for relationships within *Cyanea*? The five sections of *Cyanea*

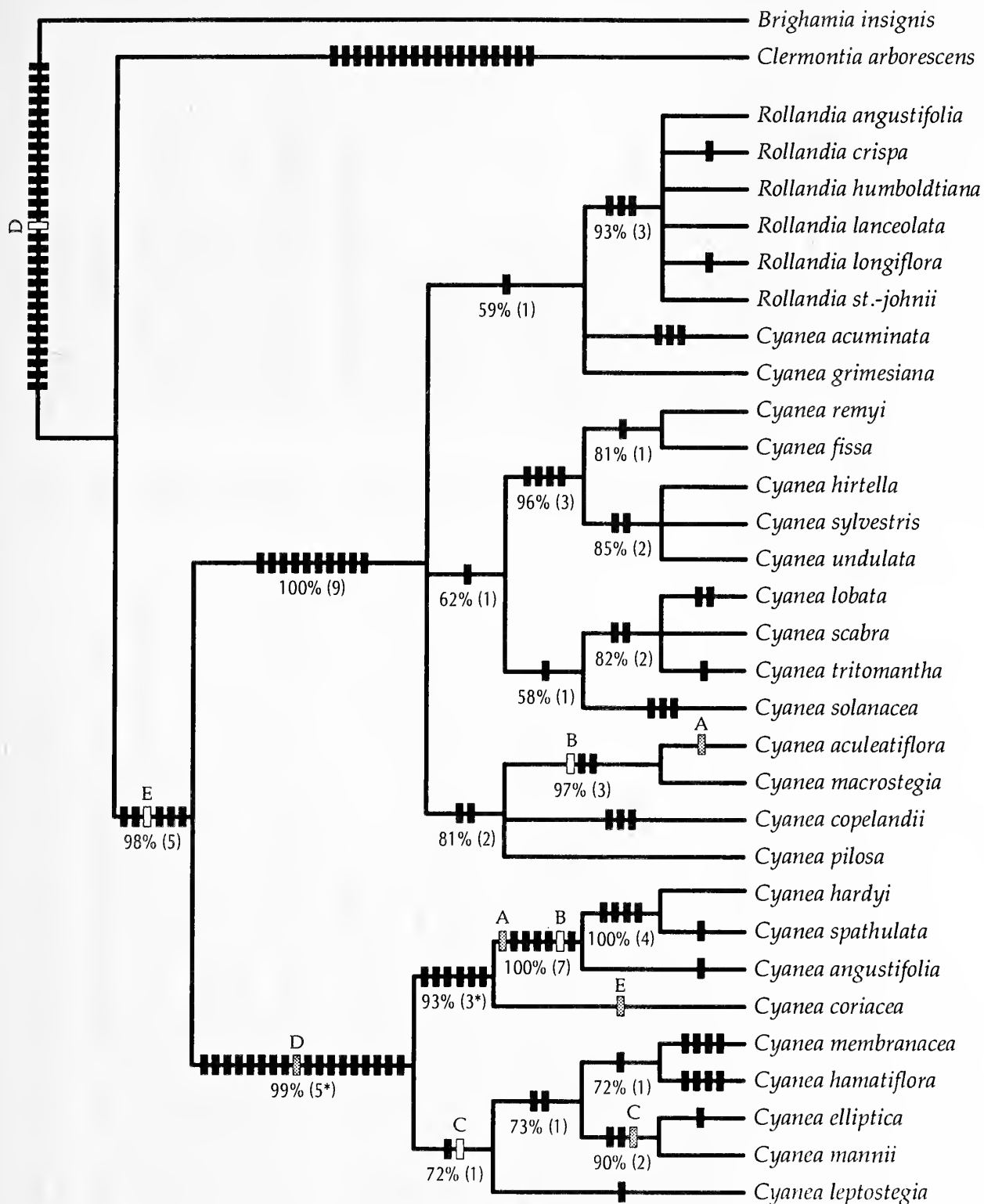


FIGURE 14.8. Cladogram showing phylogenetic relationships within *Cyanea-Rollandia*, using *Brighamia insignis* and *Clermontia arborescens* as outgroups. Consistency index = 0.974 with autapomorphies (154 steps) and 0.951 without autapomorphies (82 steps). Letters A to E identify pairs of convergent mutations. *Vertical bars* indicate synapomorphies, reflecting shared derived cpDNA restriction site gains or losses. *Hollow bars* indicate convergent site losses; *gray bars*, convergent site gains; and *solid bars*, unique site gains or losses. Bootstrap values (Felsenstein, 1985) below each node indicate the percentage of random resamplings of the cpDNA data that generate phylogenies preserving that node; decay analysis values (shown in parentheses; see Bremer, 1988) indicate the number of additional steps beyond the most-parsimonious tree needed to lose resolution at a node. Both indices reflect the relative level of support for a particular node. *Asterisks* indicate decay analysis values that are strongly affected by missing data for *C. coriacea*.

TABLE 14.3. Sources of Leaf Tissue Used in cpDNA Restriction Site Analysis of Relationships within *Cyanea* and *Rollandia*

| Species | Island ^a | Location and elevation | Date ^b | Voucher or field identification ^c |
|-------------------------------|---------------------|---|-------------------|--|
| <i>Brighamia insignis</i> | K | Kaua'i Museum, Lihu'e | 1/6 | <i>Giinnish & Sytsma</i> 3001 |
| <i>Clermontia arborescens</i> | Mo | Pepé'opae Trail, Kamakou TNC Reserve, 1,200 m | 1/10 | T. Givnish, field id |
| <i>Cyanea aculeatiflora</i> | M | Waikamoi Flume, E. Maui, 1,275 m | 1/14 | <i>Giinnish & Sytsma</i> 3002 |
| <i>Cyanea acuminata</i> | O | Hidden Valley, Ko'olau Mts., 425 m | 6/30 | J. Obata, field id |
| <i>Cyanea angustifolia</i> | O | Halawa Trail, Ko'olau Mts., 550 m | 8/27 | J. Obata, field id |
| <i>Cyanea copelandii</i> | M | Lower Waikamoi Flume, E. Maui, 1,100 m | 1/14 | <i>Giinnish & Sytsma</i> 3003 |
| subsp. <i>haleakalaensis</i> | | | | |
| <i>Cyanea coriacea</i> | K | Wainiha Valley, northern coast | 8/16 | <i>Flynn</i> 3492 |
| <i>Cyanea elliptica</i> | L | Upper Maunalei, in unnamed feeder ditch, 875 m | 9/19 | <i>Hobdy</i> 3084 |
| <i>Cyanea fissa</i> | K | Wahiawa stream valley, 675 m | 7/19 | <i>Flynn</i> 3460 |
| <i>Cyanea grimesiana</i> | O | Kalua'a Gulch, Wai'anāe Mts. | 1/1 | <i>Giinnish & Sytsma</i> 3004 |
| subsp. <i>obatae</i> | | | | |
| <i>Cyanea hamatiflora</i> | M | Ravine at head of Waikamoi Flume, E. Maui, 1,275 m | 1/14 | <i>Giinnish & Sytsma</i> 3005 |
| <i>Cyanea hardyi</i> | K | Anahola stream valley | 1/4 | <i>Smith</i> 1151 |
| <i>Cyanea hirtella</i> | K | Alaka'i Swamp Trail, 1,150 m | 7/20 | <i>Smith et al.</i> 2179 |
| <i>Cyanea leptostegia</i> | K | Koke'e State Park | 1/6 | <i>Smith et al.</i> 1135 |
| <i>Cyanea lobata</i> | M | Juvenile near former adult population, Waikapu, W. Maui | 1/14 | R. Hobdy, field id |
| <i>Cyanea macrostegia</i> | L | Shady ravine in Kaiholena Gulch, 800 m | 9/19 | <i>Hobdy</i> 3088 |
| subsp. <i>gibsonii</i> | | | | |
| <i>Cyanea mannii</i> | Mo | Upper Kawela Gulch, Kamakou TNC Reserve | 1/10 | <i>Smith et al.</i> 1160 |

| | | | | |
|-------------------------------|----|--|------|--------------------------|
| <i>Cyanea membranacea</i> | O | Kalua'a Gulch, Wai'anae Mts. | 7/2 | J. Obata, field id |
| <i>Cyanea pilosa</i> | H | Kohala Mts., upper Hamakua Ditch, above Pu'ulehua reservoir, 925 m | 7/14 | Smith et al. 2145 |
| <i>Cyanea remyi</i> | K | Wahiawa stream valley, 675 m | 7/19 | Givnish & Sytsma 3006 |
| <i>Cyanea scabra</i> | M | Hana'ula Trail, W. Maui, 1,025-1,125 m | 1/11 | R. Hobdy, field id |
| <i>Cyanea solanacea</i> | Mo | Upper Kawela Gulch, Kamakou TNC Reserve | 1/10 | Givnish & Sytsma 3007 |
| <i>Cyanea spathulata</i> | K | Alaka'i Swamp Trail | 1/2 | Smith et al. 1140 |
| <i>Cyanea sylvestris</i> | K | Hoary Head ridge, near Knudsen Gap | 1/3 | Smith & Flynn 1146 |
| <i>Cyanea tritomantha</i> | H | Kohala Mts., Hamakua district | 7/18 | L. Stemmermann, field id |
| <i>Cyanea undulata</i> | K | Wahiawa stream valley, 675 m | 7/19 | Smith et al. 2191 |
| <i>Rollandia angustifolia</i> | O | Halawa Trail, 550 m | 8/27 | Smith 2209 |
| <i>Rollandia crispa</i> | O | Hidden Valley, Ko'olau Mts., 425 m | 1/8 | Givnish 1038 |
| <i>Rollandia humboldtiana</i> | O | Moanalua Ridge, Ko'olau Mts. | 1/2 | J. Obata, field id |
| <i>Rollandia lanceolata</i> | O | Kalua'a Gulch, Wai'anae Mts. | 1/1 | J. Obata, field id |
| <i>Rollandia longiflora</i> | O | Pahole Gulch, Wai'anae Mts. | 1/9 | Givnish 1039 |
| <i>Rollandia st.-johnii</i> | O | Summit crest between 'Aiea and Halawa trails, Ko'olau Mts., 850 m | 8/27 | Smith et al. 2208 |

^aK, Kaua'i; Mo, Moloka'i; M, Maui; O, O'ahu; L, Lana'i; H, Hawai'i.

^bMonth/day (all in 1989).

^cGiven the unbranched habit and endangered status of several species and the fact that many well-known populations have been previously vouchered, in several instances we have relied as noted on field identification by our informants (supported by color slides in many cases). Vouchers are deposited at WIS.

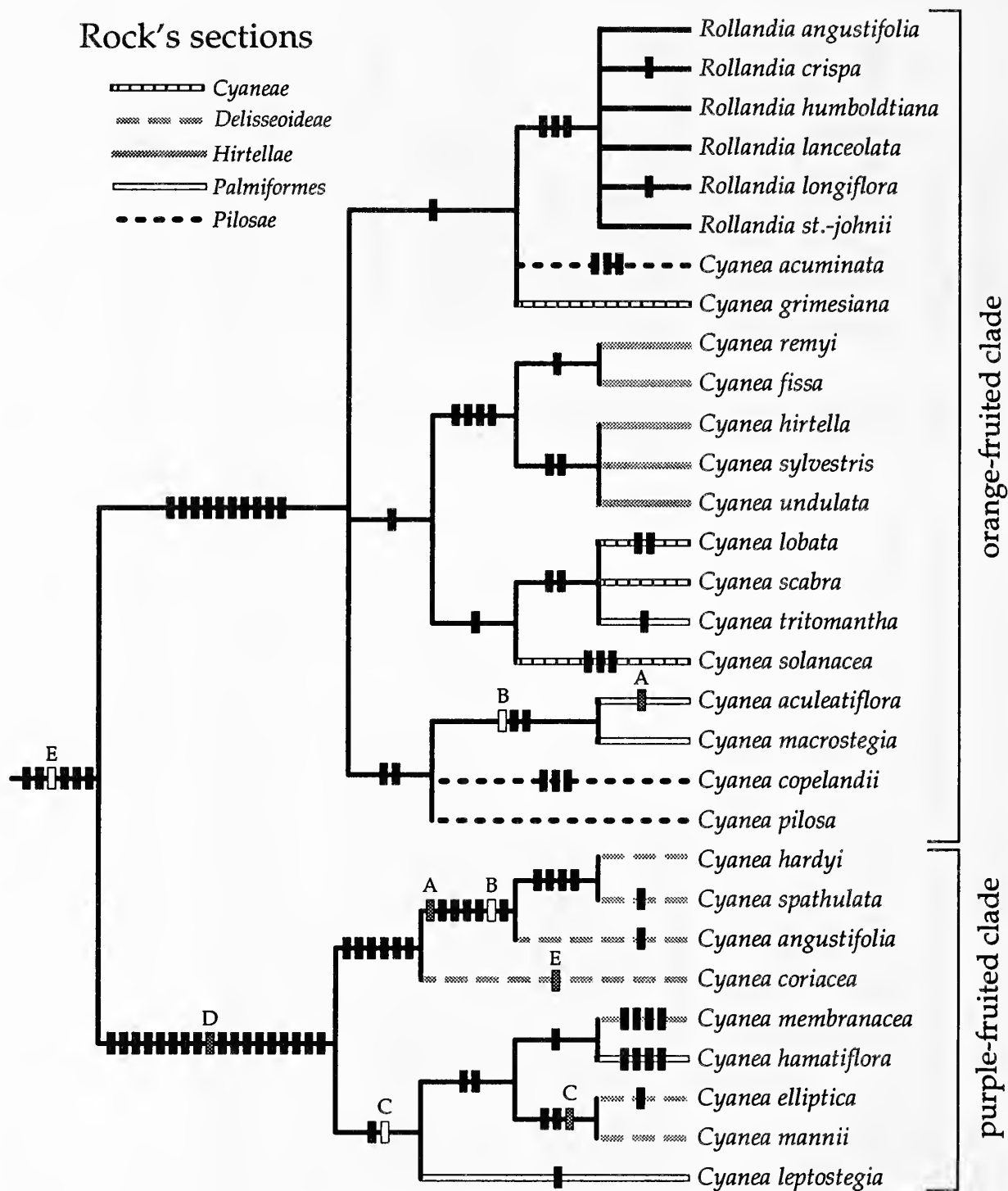


FIGURE 14.9. Morphologically defined sections of *Cyanea* (Rock, 1919) superimposed on the cpDNA phylogeny. See Figure 14.8 for explanation of symbols.

recognized by Rock (1919) on morphological grounds show only partial concordance with our molecular phylogeny (Figure 14.9). Section *Hirtellae* (unbranched treelets or small trees from Kaua‘i characterized by a tomentose corolla and calyx lobes at least as long as the calyx tube) form a monophyletic group in the cpDNA analysis, provided that the recently rediscovered *C. remyi* (poorly known to Rock) is included (Figure 14.9). Section *Delisseoideae* (characterized by minute calyx lobes like those of *Delissea*) fall into

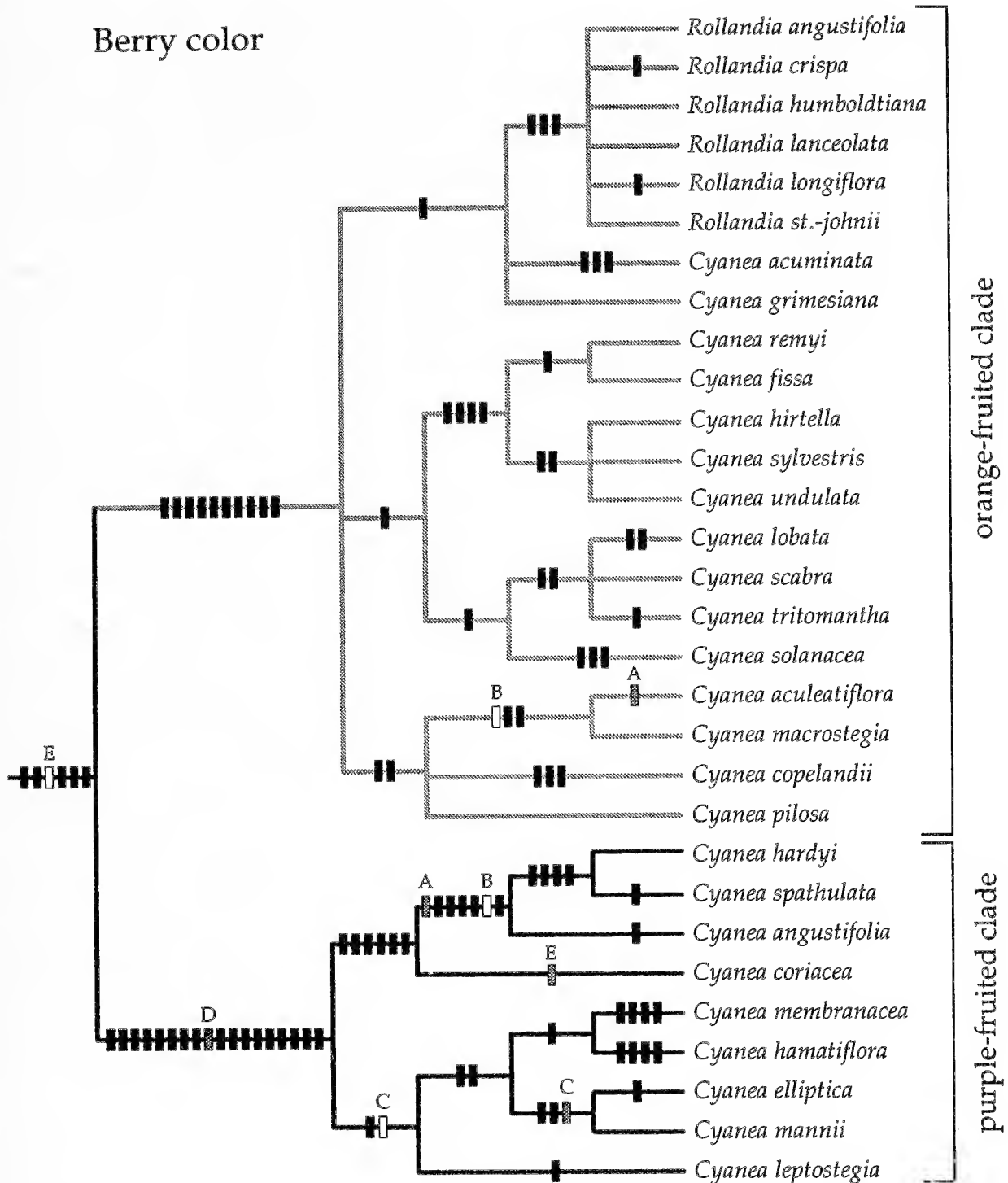


FIGURE 14.10. Berry color superimposed on phylogeny. Orange fruits, gray; purple fruits, black. *Cyanea leptostegia* has purple fruits fide Carlquist, 1974; S. Carlquist, unpubl.; T. G. Lammers, unpubl.; cf. Lammers, 1990a, and E. Knox, unpubl. See Figure 14.8 for explanation of symbols.

the second clade shown in Figure 14.9, but two nondelisseoid, palmlike species (*C. hamatiflora*, *C. leptostegia*) are also included.

Palmlike species (section *Palmiformes*) appear to have arisen on at least three separate occasions and apparently do not represent a natural group. Likewise, neither section *Cyaneae* (midsized shrubs and trees with leaves that are often toothed or divided, and with smooth corollas and

calyx lobes that equal or exceed the calyx tube) nor section *Pilosae* (subherbaceous treelets with similar calyx lobes and pubescent corollas and leaves) represent natural groupings (Figure 14.9). These conclusions clearly indicate that the sections of *Cyanea* must be revised if they are to reflect monophyletic groupings and that analyses of *Cyanea* based on morphology-based taxonomic schemes must be viewed with caution.

Certain morphological characters map fairly cleanly onto our molecular phylogeny; the best example is fruit color (Figure 14.10). The clade including the delisseoids is composed entirely of species with purple fruits; the first clade is composed almost entirely of species with orange fruits, with the presumed exception of the extinct *Rollandia purpurellifolia* (Lammers, 1990a). This difference in fruit color may simply be a phylogenetic quirk, a character of minimal selective value that demarcates the two main clades in *Cyanea*. However, it might reflect differences in ecology between the clades and represent an adaptive difference between them. Rock (1919) noted that many of the species of section *Delisseoideae*, most of which are sparsely branched from the base, tend to occur in forest edges or in drier, more open forests than those occupied by most other *Cyanea* species. Although purple fruits may be especially conspicuous to birds in such sites, they may tend to be inconspicuous in dense green shade under closed canopies, where a brighter, orange fruit may be more attractive. Whatever its basis, the characteristic difference in fruit color between clades makes it convenient to denote them as the *orange-fruited* and the *purple-fruited* clades, respectively.

ADAPTIVE RADIATION IN CYANEA

Adaptive Radiation in Relation to Flower Tube Length

We classified species of *Cyanea* and *Rollandia* into four classes based on typical corolla tube length (average of the minimum and maximum values given by Lammers, 1990a) and then superimposed flower length on phylogeny (Figure 14.11). Two patterns emerged. Perhaps the most obvious is that there is no consistent tendency for flower size to increase or decrease within a lineage (i.e., flower size is evolutionarily quite labile within *Cyanea*). This accords with some of our preliminary results (data not shown) for the genus *Clermontia*, in which the closest relative of *C. grandiflora* (with flowers among the largest in the genus) is *C. micrantha* (with flowers among the smallest).

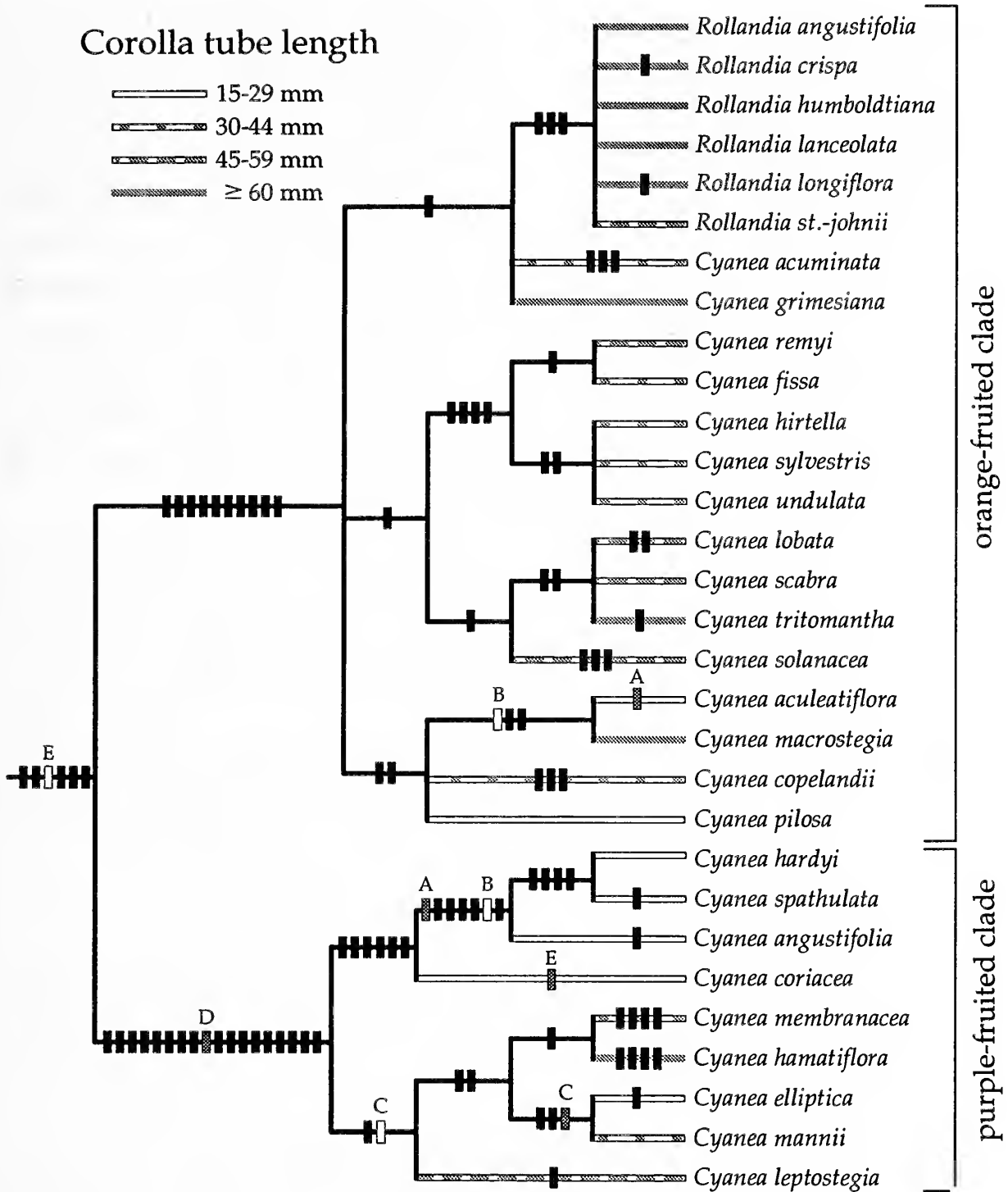


FIGURE 14.11. Corolla tube length superimposed on phylogeny. Values represent average of the minimum and maximum tube lengths reported by Lammers (1990a). See Figure 14.8 for explanation of symbols.

The *orange-fruited* clade does, however, show a greater range of variation in flower size, with a significantly greater average corolla tube length (49.5 ± 16.5 mm versus 35.7 ± 20.3 mm, $P < .05$ for a two-tailed t test, 55 d.f.). Members of this clade appear to inhabit somewhat shadier sites than those occupied by the *purple-fruited* clade (see above). This result may parallel certain findings regarding hummingbird-pollinated

plants in neotropical cloud forests. Feinsinger (1983) observed that species found in forest gaps tend to have short corolla tubes, whereas those found under closed canopies have a diversity of corolla lengths, with many species having long flowers. The long-tubed flowers in understories are often sparsely distributed and exclude all but the few long-billed hummingbirds that find it profitable to "trap-line" them; the short-tubed flowers, found in well-lit, productive gaps, are often densely aggregated and attract highly territorial, short-billed hummingbirds. Nectar thievery (via piercing the corolla) would, in our view, help select against the evolution of long flowers in gap plants, given the attraction of thieves to large aggregations of flowers and the reward associated with large amounts of nectar in flowers with long floral tubes.

The tendency for the *orange-fruited* clade to have longer flowers and, hence, a wider range of flower tube lengths may have been one of three primary factors (in addition to possessing prickles and greater dependence on forest interior birds for seed dispersal) leading to the evolution and maintenance of greater species richness in the *orange-* versus *purple-fruited* clade (50 versus 13 species). A wider range of flower lengths may have allowed species in the *orange-fruited* clade to coevolve with and partition a wider suite of honeycreepers and other avian pollinators.

Adaptive Radiation in Relation to Leaf Size and Shape

In unbranched or sparsely branched trees and treelets, leaf length essentially determines canopy diameter and, hence, the potential photosynthetic productivity of that canopy. As predicted by Carlquist (1965), we found a strong tendency for leaf length to increase with maximum plant height (Figure 14.12); taller trees must have broader crowns to sustain positive growth, given the allometry of support tissue with plant height (Givnish, 1988).

Species in the *orange-fruited* clade tend to have longer leaves (and broader crowns) at a given maximum height than do species in the *purple-fruited* clade (Figure 14.12). (A more detailed analysis of this pattern that incorporates phylogenetic relationships will be conducted with T. Garland.) This accords with the view that the *purple-fruited* species generally occupy sunnier sites than do the *orange-fruited* species and thus would require less photosynthetic tissue to support growth at a given height; to the extent that these sunnier sites are also drier (Rock, 1919), the *purple-fruited* species may also simply be unable to support the transpirational load associated with broader canopies. The un-

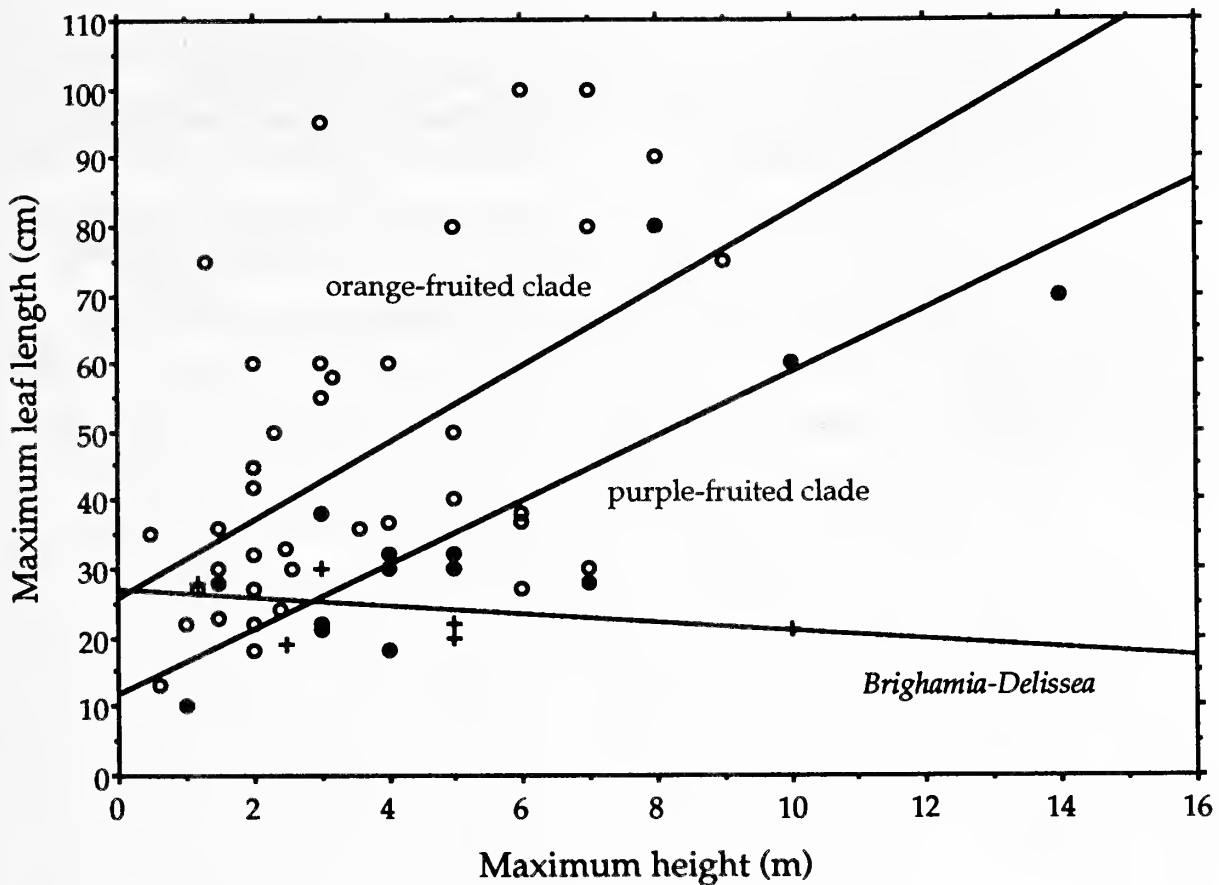


FIGURE 14.12. Maximum leaf length in relation to maximum plant height in the *orange-fruited* clade (○), *purple-fruited* clade (●), and *Brighamia-Delissea* (+). Species were assigned to the *orange-* and *purple-fruited* clades based on phylogenetic analysis (Figure 14.10) and fruit color. Lines represent LMS regressions. The *orange-fruited* clade has significantly longer leaves (and hence, broader crowns) at a given height than the *purple-fruited* clade ($P < .05$, ANCOVA), and leaf length increases more rapidly with plant height in both the *orange-* and *purple-fruited* clades than in *Brighamia-Delissea* ($P < .01$, two-tailed t tests).

branched species of *Brighamia* and *Delissea* have even narrower crowns at a given maximum height (Figure 14.12), particularly the tallest species, in accord with their occurrence in even more open and arid habitats.

Deeply toothed, lobed, or compound leaves on adult plants are restricted to the *orange-fruited* clade, based on the species surveyed to date and the berry color of the remaining taxa (Table 14.4). Such divided adult leaves are strongly associated with developmental heterophylly and vice versa, with the juvenile leaves being more deeply divided. Carlquist (1965) suggested that divided leaves may serve to spread the foliage in a thinner (and broader) presentation and thus be adaptive in shady areas. This argument does not seem compelling, as there is no obvious constraint (e.g., constant leaf tissue volume or mass) that would tie the cross-sectional thickness of leaves to area, and divided *Cyanea* leaves are

TABLE 14.4. Co-occurrence of Prickles, Marked Juvenile–Adult Heterophylly, and Divided (Coarsely Toothed, Lobed, or Compound) Adult Leaves in *Cyanea* and *Rollandia*

| Species | Prickles | Heterophylly | Divided adult leaves |
|------------------------------------|----------|--------------|----------------------|
| <i>C. aculeatiflora</i> | × | | |
| <i>C. asplenifolia</i> | × | × | × |
| <i>C. grimesiana</i> | × | | × |
| <i>C. horrida</i> | × | × | × |
| <i>C. leptostegia</i> | | × | |
| <i>C. lobata</i> | × | × | × |
| <i>C. macrostegia</i> ^a | | × | |
| <i>C. marksii</i> | × | × | |
| <i>C. mceldowneyi</i> | × | × | |
| <i>C. pinnatifida</i> | × | × | × |
| <i>C. platyphylla</i> | × | × | |
| <i>C. quercifolia</i> | × | × | × |
| <i>C. scabra</i> | × | | |
| <i>C. shipmanii</i> | × | × | × |
| <i>C. solanacea</i> | × | × | × |
| <i>C. solenocalyx</i> | × | × | |
| <i>C. stictophylla</i> | × | × | × |
| <i>C. tritomantha</i> | × | × | |
| <i>C. truncata</i> | × | | |
| <i>R. lanceolata</i> | × | × | |
| <i>R. longiflora</i> | × | × | |
| <i>R. st.-johnii</i> | × | | |

Sources: Data compiled from Rock (1919) and Lammers (1990a, 1992).

^a*Cyanea macrostegia* is roughly hispid but has no thornlike prickles.

generally not large enough to have a significant effect on the capture of sunflecks (Givnish et al., 1994).

We propose two alternative hypotheses to account for the significance of divided foliage in *Cyanea*. First, toothed, lobed, or deeply divided foliage in mature or juvenile stages may have evolved in *Cyanea* species exposed to low light levels, in parallel with the general tendencies for shade-adapted foliage to be thin (see review by Givnish, 1988), and for non-entire leaf margins to be associated with thin leaf cross sections, thus optimizing the area supported and supplied by leaf veins (Givnish, 1979). This hypothesis would account for the association of divided foliage with juveniles and with adults in the *orange-fruited* clade, in

accord with the view that the latter is adapted to somewhat shadier conditions than the *purple-fruited* clade. It would also provide an explanation for the neotenic evolution of leaf form in *C. solanacea* and related species and races documented by Lammers (1990b).

Lammers (1990b) argued that, in a series of five species and local races occupying progressively younger terrain from Moloka'i to eastern Hawai'i, there is a strong tendency for leaf outlines of each taxon to be more deeply divided than those of the corresponding adults and for the leaf outlines of the adults of each species to strongly resemble those of juveniles of the preceding species in the series (Figure 14.13). If juvenile plants of forest trees and treelets are exposed to lower light levels than adults of the same species, retention of the juvenile growth form in the neotenic adults of a daughter species should make it more fit for growth in shadier microsites than the adults of the mother species, and its juveniles should have even more deeply divided foliage. The extreme endpoint of Lammers's neotenic series, the doubly compound-leaved *Cyanea shipmanii*, occurs in extremely shady ravines on Hawai'i (Carlquist, 1980).

A second hypothesis for the evolution of divided foliage in juveniles and the orange-fruited clade would be that divided foliage served to deceive visually oriented avian browsers (now extinct) by presenting a nonlobelioid leaf outline (Givnish, 1990; Givnish et al., 1994). Fifteen of the 17 species showing marked developmental heterophylly are also armed with prickles on their juveniles leaves or stems (Table 14.4), strongly suggesting that heterophylly may indeed have been involved in defense against herbivory (Givnish et al., 1994). This hypothesis may also provide a general explanation of insular heterophylly (Friedmann and Cadet, 1976), the relatively high incidence of juvenile-adult leaf dimorphism in the floras of New Zealand, New Caledonia, Madagascar, and the Mascarene Islands; each of these isolated oceanic islands and archipelagoes was populated by various groups of flightless birds (moas, *Sylviornis*, elephant birds, and possibly dodos, solitaires, or rails, respectively) that acted as the primary terrestrial browsers (Givnish et al., 1994).

The visual defense hypothesis is compatible with the development of juvenile foliage on short stems near the ground and on mechanically wounded stems, where the plants would be visible and accessible to large browsing birds. This hypothesis is consistent with an association of divided foliage with species of the *orange-fruited* clade, because selection for antiherbivore defenses should be particularly strong in shady, unpro-

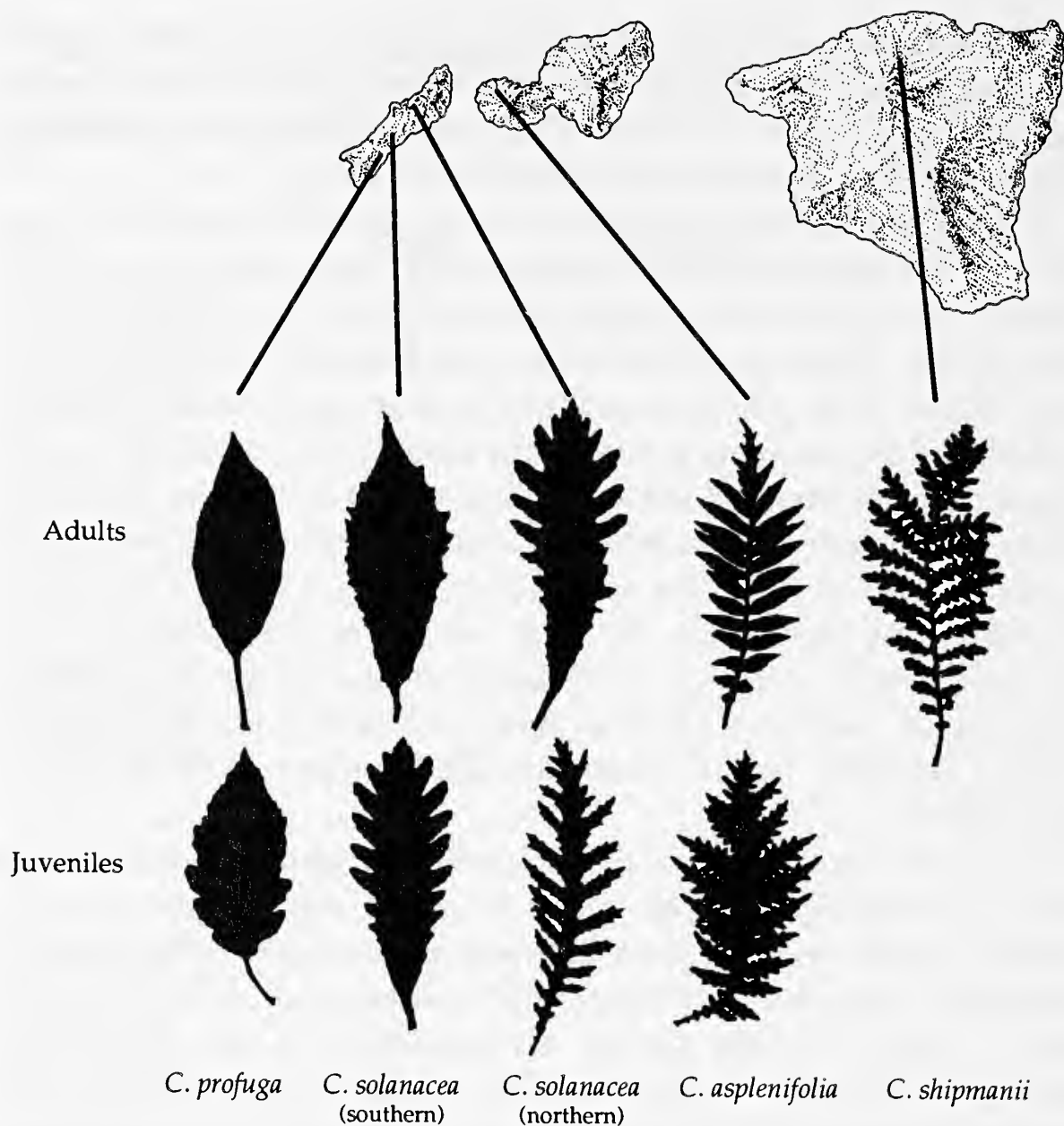


FIGURE 14.13. Apparent paedomorphosis of leaf form in a suite of species occupying a sequence of progressively younger terrains from southeastern Moloka'i to Mauna Kea on Hawai'i (redrawn from Lammers, 1990b). Note that the juvenile foliage of each species is more divided than the adult foliage of the same species and that the adult foliage of each species strongly resembles the juvenile foliage of the preceding species in the sequence.

ductive environments (Coley, 1983; Givnish, 1990). It is compatible, as well, with the production of divided foliage in shadier conditions, either because it is mechanically more efficient (see above) or because it might increase handling time or enhance visual mimicry of heavily defended tree ferns. Finally, selection for perfection of visual and mechanical defenses against herbivores could provide the selective force driving the neotenic evolution of leaf form and prickly development in the *Cyanea solanacea* clade (Figure 14.13).

Adaptive Radiation in Relation to Prickles

Muricate or aculeate stems and leaves are restricted to the *orange-fruited* clade among the species surveyed (Figure 14.14); they are known from 20 species in all (Table 14.4), none of which bear purple fruit. Prickles evolved at least four times within the *orange-fruited* clade: in the *Cyanea*

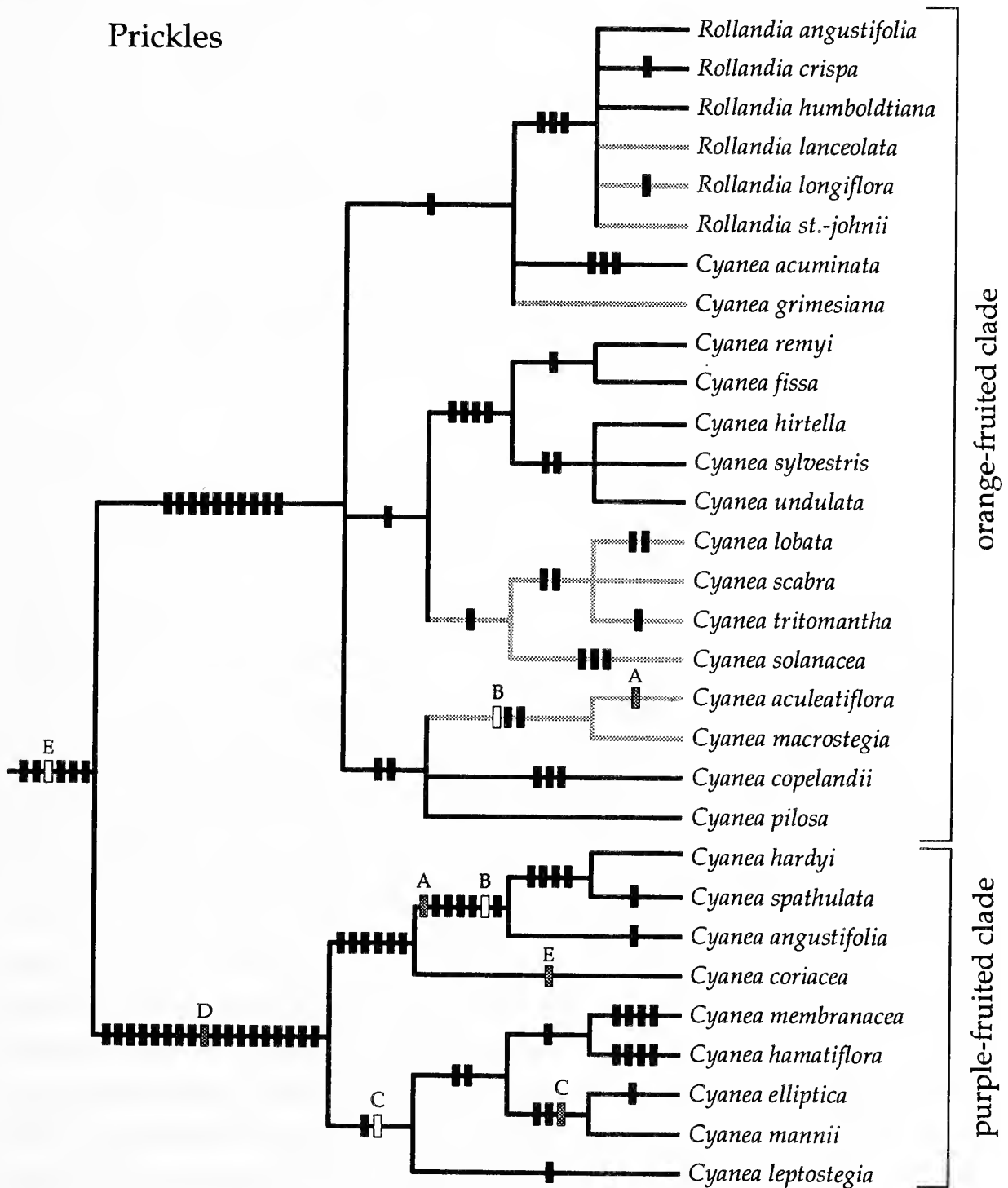


FIGURE 14.14. Possession of prickles (gray) superimposed on the cpDNA phylogeny of *Cyanea-Rollandia*. Prickles arose at least four times independently (indicated in gray), involving two origins each on O'ahu and Maui (see Figure 14.16). See Figure 14.8 for explanation of symbols.

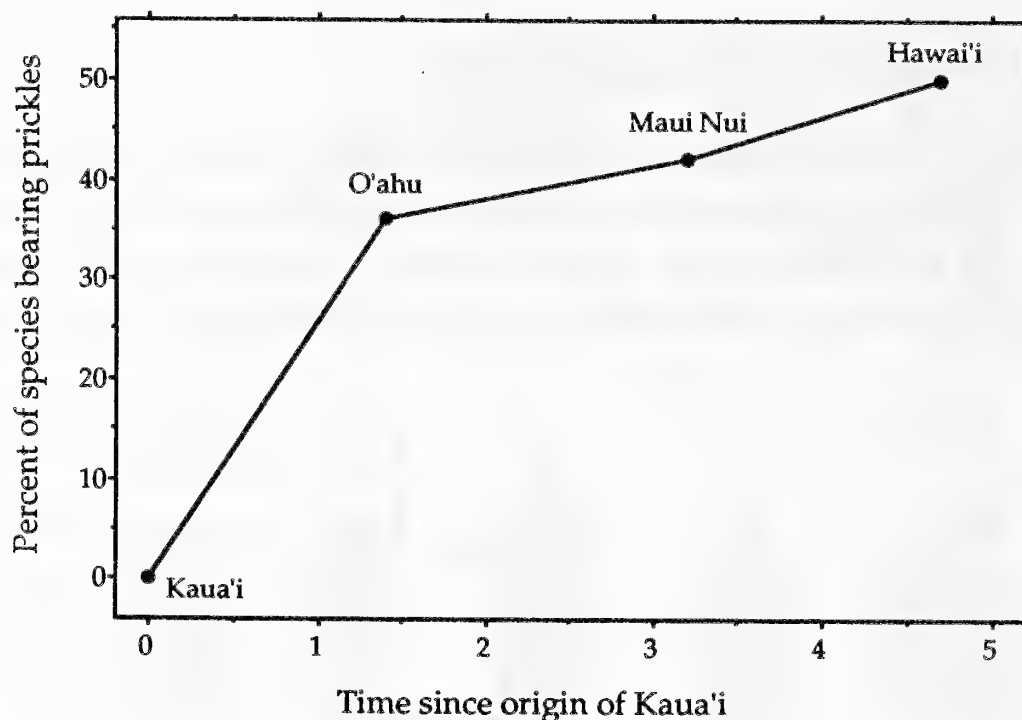


FIGURE 14.15. Percentage of species of *Cyanea-Rollandia* bearing prickles as a function of the time of island origin, in millions of years since the origin of Kaua'i.

solanacea-lobata-scabra-tritomantha subclade; in the *C. aculeatiflora-macrostegia* subclade; in *C. grimesiana*; and in the common ancestor of *Rollandia lanceolata*, *R. longiflora*, and *R. st.-johnii*. The great majority of prickly species occur on relatively young islands, and the fraction of such species (prickly per total) on each island decreases with island age (Givnish et al., 1994): 0 of 16 on Kaua'i, 5 of 14 on O'ahu, 11 of 26 on the Maui Nui complex, and 6 of 12 on Hawai'i (Figure 14.15).

One explanation for this pattern would be that the ancestors of the flightless geese and moa-nalos that might have exerted selective pressure for prickly stems and leaves in *Cyanea* first appeared on O'ahu, then colonized to younger islands (Givnish et al., 1994). An alternative, somewhat more complex hypothesis would be that the avian browsers first arrived on O'ahu and caused the evolution of prickly *Cyanea* there. Subsequently, the herbivores spread throughout the chain unopposed, but *Cyanea* dispersed mainly to newly formed islands to the southeast (see below). Presumably, members of prickly lineages would have been more likely to establish themselves, radiate, and produce colonists that colonized to the next island, favoring an increase in the incidence of developing prickles by species-level selection (Stanley, 1975), as well as by traditional natural selection operating within populations. Both mechanisms would require that herbivores first colonize O'ahu or at least first exert selective pressure on *Cyanea* there (Givnish et al., 1994).

In fact, one of the seven flightless avian browsers, *Chelychelynechen quassus*, occurred on Kaua'i (Olson and James, 1991). *Chelychelynechen* possessed a remarkable tortoiselike bill, unlike that of the other flightless geese and moa-nalos; we infer that it may have been more adapted to grazing than browsing. Other moa-nalos have mandibles with toothlike projections and are strongly decurved, which would increase the range of cutting forces exerted along their length (Olson and James, 1991). In the Hawaiian archipelago, the six flightless avian browsers (*Thambetochen*, *Ptaiochen*, *Geochen*, and unnamed taxa for which browsing is inferred from body size), excluding *Chelychelynechen* from Kaua'i, are known only from the younger islands, with two species each on O'ahu, the Maui Nui complex, and Hawai'i (Olson and James, 1991).

The relatively low number of species (six) in the purple-fruited clade on islands younger than Kaua'i may be because protective prickles did not evolve in this lineage. It is possible that the divided juvenile foliage of *Cyanea leptostegia*, a purple-fruited species from Kaua'i, may have arisen as a result of adaptation to shade rather than to visually orienting browsers.

PHYLOGENY IN RELATION TO GEOGRAPHY

Most species of *Cyanea* and *Rollandia* (57 of 63) are restricted to single islands, so the group provides outstanding material for the study of geographic speciation. Among the species studied thus far, there is a fairly strong association of phylogeny with geographic distribution, and some specific dispersal events—presumably a result of frugivorous birds carrying seeds internally from one island to another—are required to account for the observed pattern of diversification (Figure 14.16).

For example, within the *hardyi* sublineage of the *purple-fruited* clade, three of the four species (*Cyanea coriacea*, *C. hardyi*, *C. spathulata*) are known only from Kaua'i, whereas *C. angustifolia* is found on O'ahu, Moloka'i, Lana'i, and West Maui. For this clade, parsimony would indicate one inter-island dispersal event associated with speciation from Kaua'i to O'ahu followed by further colonization to younger islands without speciation.

The *hardyi* clade is also of interest in terms of how the species have diverged in order to coexist. All four species show very little divergence in habit, height, leaf length, or flower size (Lammers, 1990a); they essentially appear ecologically equivalent. Yet they differ dramatically in the

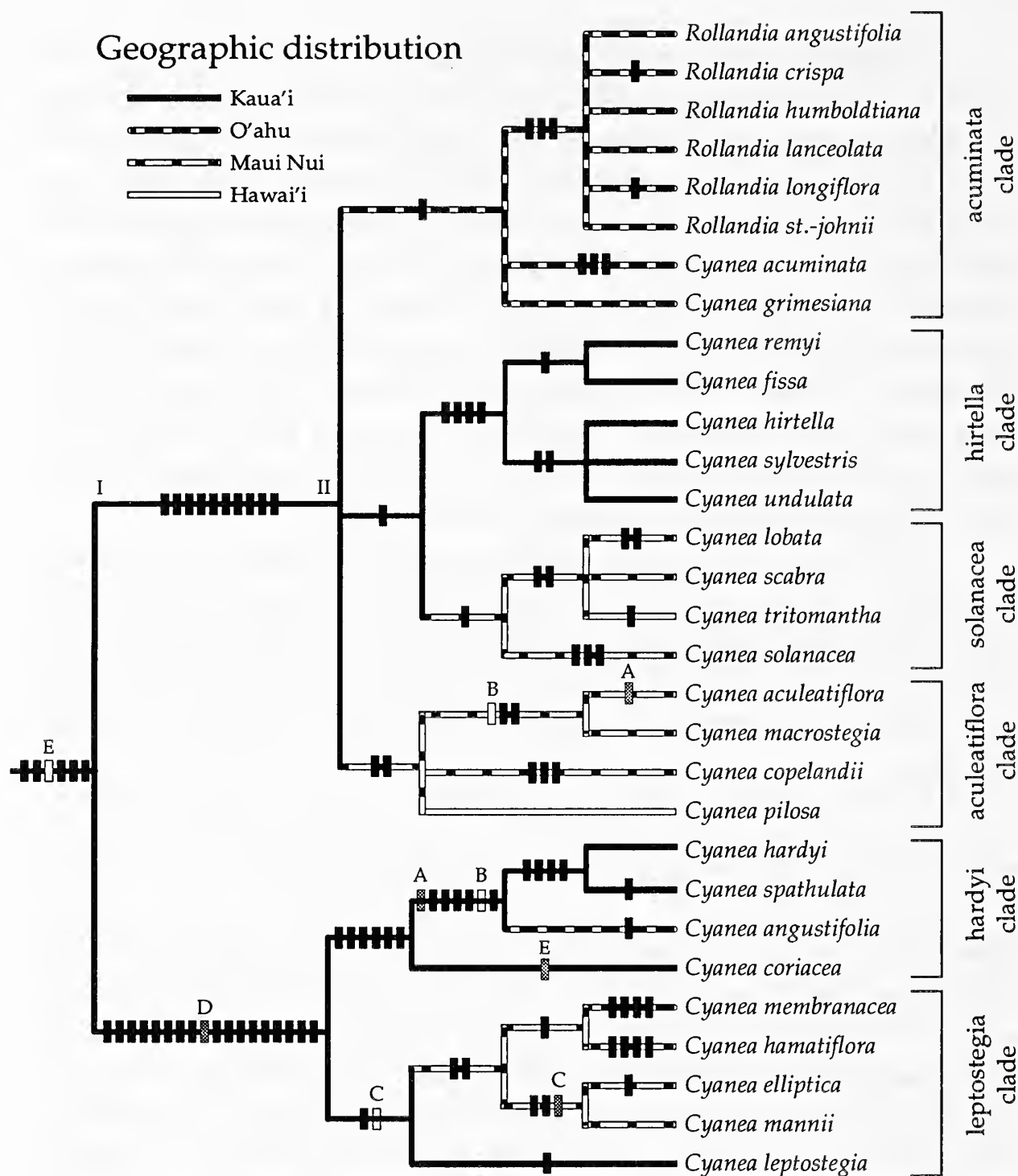


FIGURE 14.16. Geographic distribution superimposed on cpDNA phylogeny. See Figure 14.8 for explanation of symbols.

elevational ranges they occupy (Figure 14.17). The basal taxon (*Cyanea coriacea*) is restricted to low-elevation forests on Kaua'i. The next species (*C. angustifolia*) occurs from low to middle elevations on O'ahu. *Cyanea angustifolia* occupies an elevational range equivalent to that occupied by *C. coriacea* and *C. hardyi* on Kaua'i; these species partition that island elevationally, with *C. hardyi* restricted to middle elevations (300 to 700 m). Finally, *C. spathulata* occupies high-elevation habitats (700 to 1,200 m). Overall, this pattern suggests a taxon cycle (Wilson,

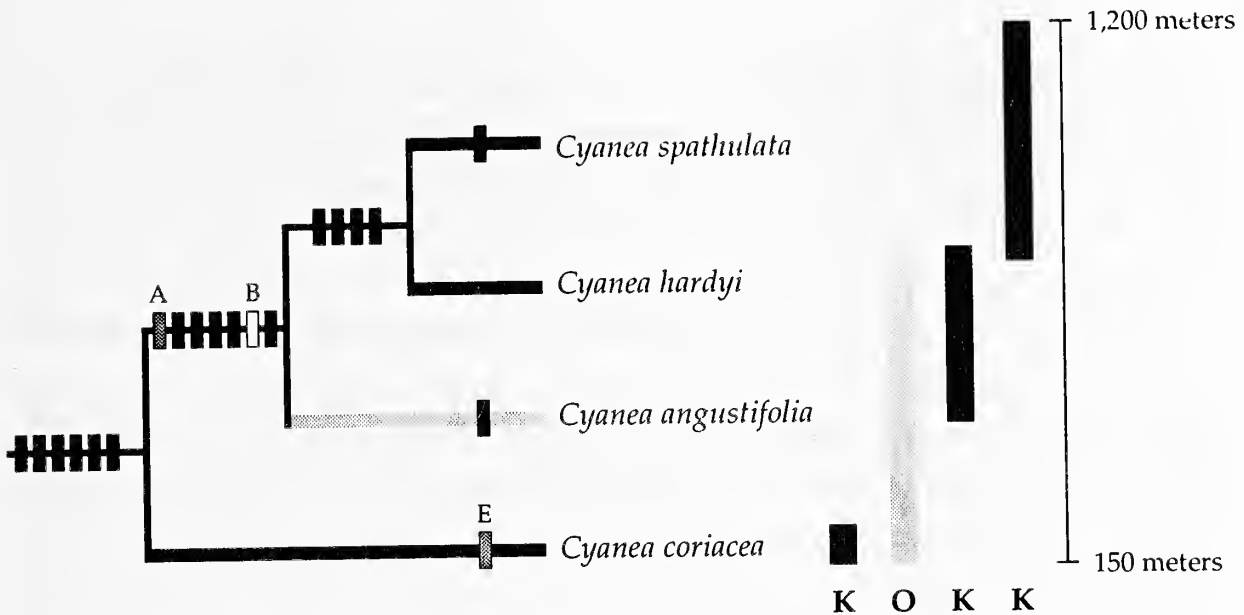


FIGURE 14.17. Elevational and geographic distribution (*right*) in relation to phylogeny within the *hardyi* clade (see text). K, Kaua'i; O, O'ahu. See Figure 14.8 for explanation of symbols.

1961) leading from an initial invasion of low-elevation sites to progressive colonization of higher elevations, with divergence in elevational preference promoting the origin and maintenance of diversity within this clade. We do not know the phylogenetic position of *C. fauriei*, the last member of section *Delisseoideae* on Kaua'i, within the *hardyi* clade, where preliminary cpDNA data place it. However, the elevational range of *C. fauriei* straddles the gap between those of *C. coriacea* and *C. hardyi* (Lammers, 1990a). The leaves of *C. fauriei* are 4 to 9 cm wide, 6 to 12 cm wide in the low-elevation *C. coriacea*, 2.5 to 5 cm wide in the mid-elevation *C. hardyi*, and 1 to 3 cm wide in the high-elevation *C. spathulata*. This sequence of leaf width follows a typical trend of declining leaf width with increasing elevation on wet tropical mountains (Grubb, 1977; Givnish, 1987).

Biogeography of the *purple-fruited* Clade

In our analysis, the basal geographic condition for the *Cyanea-Rollandia* lineage is inferred to be Kaua'i. This conclusion is based on three points: the co-occurrence of the two sister groups to the *Clermontia-Cyanea-Rollandia* clade (*Brighamia* and *Delissea*) only on Kaua'i, Ni'ihau, and Lana'i (Lammers, 1990a); the co-occurrence of the two subgenera of *Delissea* only on Kaua'i, identifying Kaua'i as the basal condition for that genus and hence for *Brighamia-Delissea*; and the co-occurrence of all five genera only on Kaua'i (see Figure 14.7). Second, Kaua'i is also the basal

condition for the *purple-fruited* clade, based on the fact that the two species that are sister to the other taxa in each of the two sublineages, *Cyanea coriacea* in the *hardyi* clade and *C. leptostegia* in the *leptostegia* clade, are restricted to Kaua'i, as are two of the remaining three species of the *hardyi* clade. To simplify discussion, Kaua'i is considered the basal condition for the *purple-fruited* and *Cyanea-Rollandia* clades. We do not exclude the possibility that each group actually originated on an older island to the northwest, now eroded below the appropriate elevation to support mesic forest. Indeed, current estimates place the origin of certain Hawaiian lineages of *Drosophila* 10 to 30 million years ago (Ma) (Thomas and Hunt, 1991; DeSalle, 1992) and the origin of the honeycreepers 15 to 20 Ma (Sibley and Ahlquist, 1982; see also Tarr and Fleischer, this volume, Chapter 9), long before Kaua'i existed. The biogeography of the two sublineages within the *purple-fruited* clade can be summarized below.

Hardyi clade.—The argument given previously requires a Kaua'i-to-O'ahu dispersal event to account for the origin of *Cyanea angustifolia* on O'ahu (see Figure 14.16). Also, *C. angustifolia* most likely dispersed from O'ahu to the Maui Nui complex (see Table 14.1). Several other scenarios could account for the present-day distribution of *C. angustifolia*, but in the absence of genetic information on the non-O'ahu populations, the one proposed is the most parsimonious in terms of the number of dispersal events.

Leptostegia clade.—Given the occurrence of *Cyanea elliptica*, *C. hamatiflora*, and *C. mannii* on the once-interconnected islands of the Maui Nui complex (see Table 14.1), it is parsimonious to assume that they and *C. membranacea* of O'ahu share a common ancestor from Maui Nui. This implies a dispersal event from Kaua'i to the Maui Nui complex to account for the origin of the sister group to *C. leptostegia* and a subsequent colonization from the Maui Nui complex to O'ahu to account for *C. membranacea* (see Figure 14.16). Also, a subsequent dispersal of *C. hamatiflora* from Maui to Hawai'i seems quite likely, to account for the presence of *C. hamatiflora* in both East Maui and the Kona district of the island of Hawai'i (see Table 14.1) and for the subsequent origin of the (now-extinct) *C. giffardii*. *Cyanea hamatiflora* appears to be the closest relative of *C. giffardii* because these are the only two *Cyanea* species with purple fruits to occur on Hawai'i, and more important, *C. giffardii* shares with *C. hamatiflora* a greater number of derived morphological character states than it does with any other species in the *purple-fruited* clade, including long corolla tubes (60 to 80 mm versus 20 to 55 mm), large

berries (25 to 45 mm diameter versus 6 to 12 mm), broad (14 to 15 mm maximum versus 2 to 12 mm) cuneate leaves, and a tall (5 to 10 m) unbranched growth form (these last traits are also shared with *C. leptostegia*).

Biogeography of the *orange-fruited* Clade

The basal condition for this clade is assumed to be Kaua'i (or an older island), based on the basal condition for *Cyanea-Rollandia* as a whole, the basal condition for the *purple-fruited* clade, and the relative distribution of cpDNA mutations within both the *purple-* and *orange-fruited* clades. Parsimony identifies Kaua'i as the basal condition ("I" in Figure 14.16) in the lineage defining the *orange-fruited* clade but leaves unresolved the condition at the end of that lineage ("II" in Figure 14.16), at the point where it split into several sublineages. Based on the relative distribution of mutations in the *purple-fruited* lineage before versus after dispersal from Kaua'i (see above) and in the *orange-fruited* lineage before versus after the radiation of that lineage, it is reasonable to assume that Kaua'i was the island from which that radiation took place (i.e., Kaua'i is the condition at point "II" in Figure 14.16). Given this assumption, several dispersal events are indicated for the four sublineages of the *orange-fruited* clade.

Acuminata clade.—The origin of this lineage requires a simple Kaua'i-to-O'ahu dispersal event. Subsequent dispersal events from O'ahu to the Maui Nui complex and from Maui Nui to Hawai'i would be required to account for the sparser presence of *Cyanea grimesiana* in these latter two areas.

Hirtella clade.—No inter-island dispersal is required to account for the distribution of this lineage, whose extant species are restricted to Kaua'i. However, a Kaua'i-to-O'ahu dispersal would be required to account for the origin of the extinct *Cyanea truncata* on O'ahu, which shared an unusual, broad leaf shape only with *C. remyi* of Kaua'i, a presumed close relative of the morphologically defined section *Hirtellae*, which are otherwise restricted to Kaua'i (Lammers, 1990a; T. G. Lammers, unpubl.).

Solanacea clade.—In contrast, the most-parsimonious basal condition for the *solanacea* clade is the Maui Nui complex. Thus, a Kaua'i-to-Maui Nui dispersal is required for this group's common ancestor (see Figure 14.16). A subsequent Maui Nui-to-Hawai'i dispersal is required for the origin of *Cyanea tritomantha*. If one accepts Lammers's (1990b) morphological argument that *C. shipmanii* is most closely related to the

C. solanacea-quercifolia-asplenifolia group on the Maui Nui complex, then an additional Maui Nui-to-Hawai'i dispersal event is indicated.

Aculeatiflora clade.—One dispersal event from Kaua'i to the Maui Nui complex is needed to account for the common ancestor of the *aculeatiflora* clade, followed by two dispersals from Maui Nui to Hawai'i to account for the occurrence of *Cyanea copelandii* on the island of Hawai'i and for the origin of *C. pilosa*.

Summary of Inter-island Dispersal

Figure 14.18 summarizes our best estimate regarding the minimum number of inter-island dispersal events (15) required to account for diversification within *Cyanea*, based on inferences from molecular data supplemented

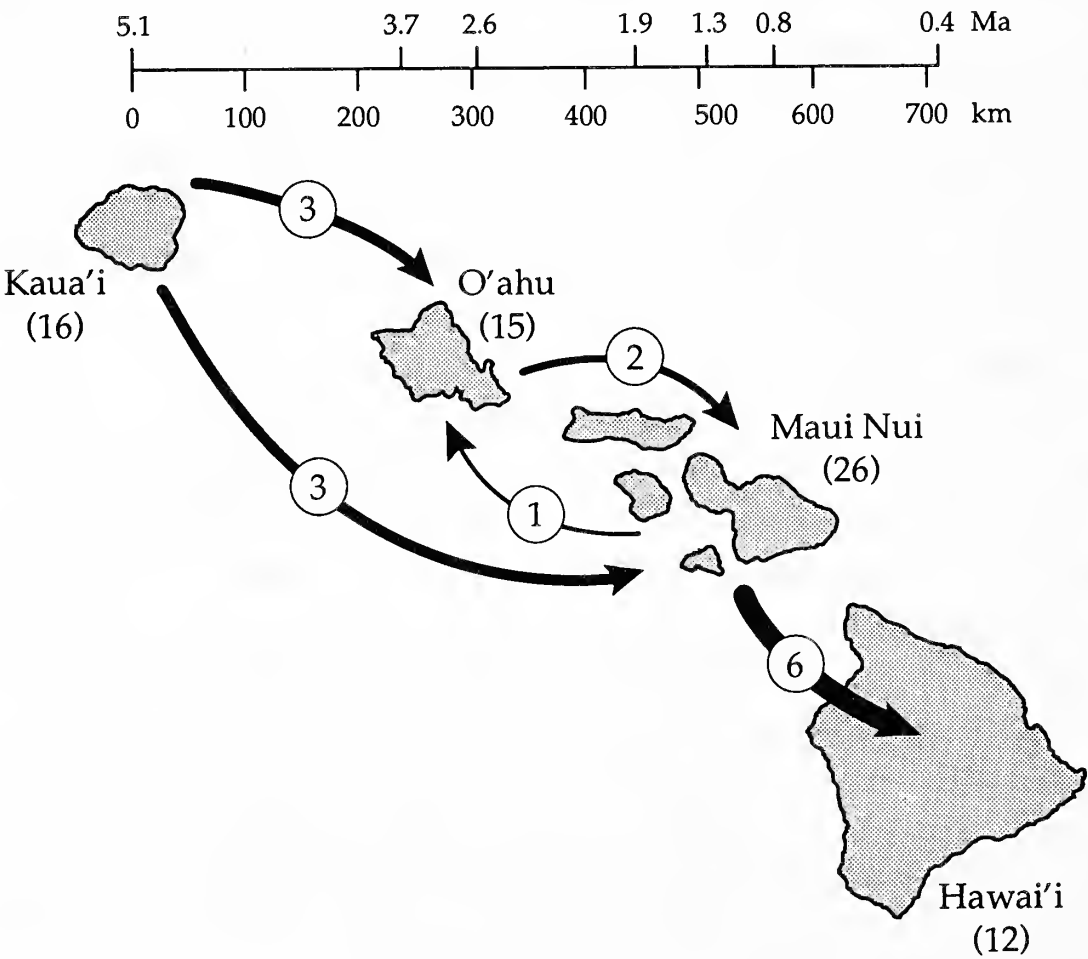


FIGURE 14.18. Minimum number of inter-island dispersal events required to account for diversification of 35 species and 40 populations of *Cyanea-Rollandia* (see text), illustrating a general tendency for dispersal from one island to the next younger island in the archipelago. Width of each arrow is proportional to the number of dispersal events between the corresponding pair of islands; the number of species found on each island or island group is indicated in parentheses.

by comparative morphology. As more nodes in the phylogeny are resolved with additional data and species of *Cyanea* added to our analysis, the number of required dispersal events will almost surely increase. Nevertheless, the biogeographic pattern now apparent is similar in many respects to that seen in the much more intensively studied *Drosophila* and silversword alliance, with dispersal mainly proceeding from one island to the next younger island in the chain (Carson, 1983a; Carr et al., 1989; Baldwin, 1992). This pattern is generally thought to reflect the greater chance of establishment and subsequent radiation by colonists on nearby, newly formed, relatively unoccupied islands created to the southeast as the oceanic crust moves past the Hawaiian hot spot. An apparent exception to this rule is the slightly greater number (three) of events from Kaua'i to the Maui Nui complex relative to the number (two) of events from O'ahu to the Maui Nui complex, but this may be an artifact of having examined relatively few of the O'ahu taxa thus far.

The diversity of *Cyanea* results partly from inter-island dispersal events, isolating populations on different islands, and partly from the isolation of populations within islands by a variety of means, including (1) dispersal to new areas of moderate elevation formed by volcanism (e.g., Wai'anae and Ko'olau Mountains on O'ahu, and Pu'u Kukui and Haleakala on Maui); (2) dissection of existing landscapes by erosion, subsidence, or changes in sea level (e.g., Lana'i, Moloka'i, and Maui in the Maui Nui complex); and (3) formation of *kipuka* by lava flows (e.g., possibly *C. giffardii* on Hawai'i, which was restricted to a single *kipuka* near Glenwood). Given that we have invoked 12 (of 15) inter-island dispersal events to account for 34 species, an additional 22 speciation events within islands would be required to account for the diversity of the group considered to date.

Time and Island of Origin

At present, our molecular data are probably inadequate for a precise analysis of the time of origin of the common ancestor of *Cyanea*. However, a regression analysis of the data currently available suggests an origin on an island somewhere between Nihoa and French Frigate Shoals, 8.7 to 17.4 Ma, well before Kaua'i, the oldest high island at present, emerged approximately 5.1 Ma.

The method adopted involves estimating the average number of restriction site mutations down each lineage subsequent to an identified dispersal event, then relating that divergence to the geologic age (Clague

and Dalrymple, 1987) of the younger island to calculate mutations per unit time. There are two obvious methods of relating the time of dispersal to the geologic age of the younger island. A "conservative" approach would assume that, on average, the dispersal event took place halfway through the lifetime of the younger island. This may not be biologically reasonable, however, in that colonizations early in an island's existence may be more likely to succeed than colonizations that occur later, after more competitors and predators have arrived. Thus, an "open ground" approach would assume that dispersal took place soon after the origin of the younger island. Clearly, the open ground approach will yield a time of origin twice that given by the conservative approach.

There are two Kaua'i-to-O'ahu dispersal events of a maximum age of 3.7 million years for which we have restriction site data, involving mutation subsequent to the origin of the *acuminata* clade and the clade including *Cyanea angustifolia*, *C. hardyi*, and *C. spathulata* (see Figure 14.16). Counting mutations down each lineage separately, summing, and dividing by the total number of species/lineages involved (11), we obtain an average of 5.6 mutations per lineage.

There were three dispersals from Kaua'i to the Maui Nui complex no more than 1.9 Ma, involving dispersal before the origins of the *solanacea* clade, the *aculeatiflora* clade, and the *Cyanea elliptica-hamatiflora-mannii-membranacea* group. These yield an average of 4.8 mutations along the lines leading to each species, subsequent to inter-island dispersal.

There was only one back-dispersal from the Maui Nui complex to O'ahu, also no more than 1.9 Ma, involving the origin of *Cyanea membranacea*, which shows three mutations since its divergence from its common ancestor with *C. hamatiflora*. There were two dispersals from the Maui Nui complex to Hawai'i no more than 0.4 Ma involving the origins of *C. pilosa* and *C. tritomantha*, which show an average of 0.5 mutations since their divergence from ancestors they share with each of their respective relatives.

The best linear fit to these data is 3.03 and 1.52 mutations per million years under the conservative and open ground assumptions, respectively ($r^2 = 0.82$). The average number of mutations down each species lineage (counting the relatively undifferentiated *Rollandia* once) since the origin of the common ancestor of the extant species of *Cyanea* would be 26.4, yielding times of origin of 8.7 Ma and 17.4 Ma under the conservative and the open ground assumptions, respectively. The former estimate would place the origin of *Cyanea* (and its divergence from a

common ancestor with *Clermontia*) when Nihoa was a high island, ca. 400 km northwest of Kaua'i; the open ground estimate points instead to an origin on French Frigate Shoals, 1,100 km northwest of Kaua'i, when they formed a high island. The fleshy-fruited clade as a whole appears to have arisen 3.3 to 6.6 million years earlier, which could have been on an island an additional 275 to 550 km further northwest, based on the 10 mutations from the origin of the fleshy-fruited clade to the divergence of *Cyanea-Rollandia* from *Clermontia* (see Figure 14.7). These estimated times of origin for *Cyanea* and the fleshy-fruited clade correspond to portions of the Hawaiian chain in which two to three hot spots were active simultaneously, presumably creating fairly extensive high islands similar to Maui Nui and Hawai'i, which were created by the double hot spot that is currently active (Clague and Dalrymple, 1987). Although the total amount of genetic divergence among extant species of *Cyanea-Rollandia* is much greater than that seen in *Brighamia*, *Clermontia*, or *Delissea*, the total amount of divergence down each lineage is roughly comparable (see Figure 14.7), justifying our extrapolation of mutation rates in *Cyanea-Rollandia* to the entire clade. Contrary to Lammers (this volume, Chapter 15), we believe that the low amount of genetic divergence within *Clermontia* reflects not its recent origin on Hawai'i (counterindicated by our analyses showing the extensive chloroplast DNA evolution in *Clermontia* since its divergence from *Cyanea*) but rather the repeated extinction of basal species, leaving only the current species, which show a pattern of radiation from Maui and Hawai'i.

Our estimates of the time of origin of *Cyanea* are admittedly crude but are the first such estimates for a Hawaiian plant group and among the very few for any plant group (see also Wolfe et al., 1989; Sytsma et al., 1991). They indicate that *Cyanea* (including *Rollandia*) had 8.7 to 17.4 million years to coevolve with its avian pollinators, frugivores, and (at least for the past 3.7 million years) herbivores and to undergo massive radiations in leaf form, flower morphology, growth habit, and prickliness. Given that the divergence of the *Brighamia-Delissea* clade from *Clermontia-Cyanea-Rollandia* occurred even earlier, it is clear that lobelioid coevolution with avian pollinators and frugivores has proceeded even longer, perhaps as long as 24 million years. Sibley and Ahlquist (1982) estimated from molecular evidence that the Hawaiian honeycreepers, likely to have been the most important group for both pollination and seed dispersal of the baccate lobeloids, originated at least 15 to 20 Ma (cf. Tarr and Fleischer, this volume, Chapter 9). This date is

consistent with the honeycreepers coevolving at an earlier stage with the radiation of the baccate lobelioids proposed here.

SPECIES RICHNESS AND EXTINCTION

With the exception of Maui, the four largest islands support roughly the same number of species of *Cyanea* (including *Rollandia*): 15 on Kaua‘i, 14 on O‘ahu, 21 on Maui, and 12 on Hawai‘i (Figure 14.19) (mean = 15.5 ± 3.9 species). The apparent excess of species on Maui may be partly explained in terms of the invasion of dry leeward forests, a novel habitat for *Cyanea*, by four species there. With the exception of Hawai‘i, *Clermontia* generally has far fewer species (6.8 ± 4.6 species) on each of these islands, and only one-third as many species as *Cyanea* overall (see Table 14.1; Figure 14.19). Two key questions arise: Why do roughly 15 species of *Cyanea* occur on each large island? And why are there so many more species of *Cyanea* than of *Clermontia*?

The first question is an intriguing puzzle for which no definite answer can yet be given. We have explored various constraints on “community assembly,” and some patterns do emerge. For example, two to four palmlike species have evolved on each large island. Species that span nearly the entire range of corolla tube lengths have arisen on each island, although the average flower size on Kaua‘i is significantly less than that of species found on younger islands (see Figures 14.5 and 14.6). Yet, we have been unable to develop a model to predict exactly which combinations of growth forms, elevation ranges, and leaf and flower morpholo-

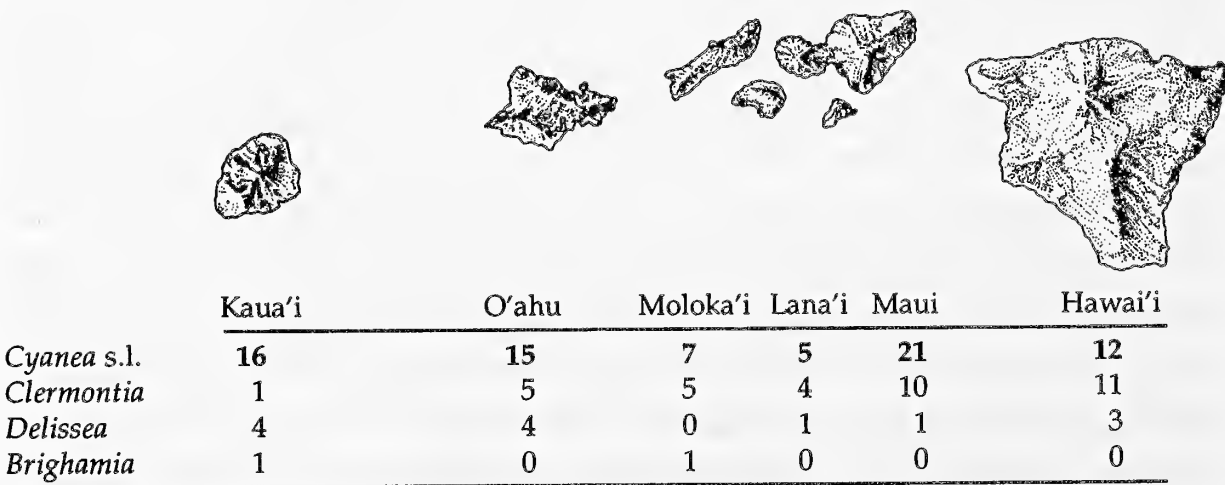


FIGURE 14.19. Geographic variation in the number of species in each genus of the baccate lobelioid alliance in the Hawaiian archipelago.

TABLE 14.5. Summary of Primary Ecological Differences between *Cyanea* (including *Rollandia*) and *Clermontia*

| | <i>Cyanea</i> | <i>Clermontia</i> |
|-----------------------------|------------------------|-----------------------|
| Habitat | Forest interiors | Edges, gaps |
| Growth form | Unbranched | Branched |
| Corolla | Cut halfway to base | Cut to base |
| Fruit | Small (ca. 15 mm) | Large (ca. 30 mm) |
| Dispersal agent | Forest interior birds? | Forest edge birds? |
| Inferred dispersal capacity | Low | Relatively high |
| Geographic distribution | Narrowly endemic | Relatively widespread |
| Elevational distribution | Relatively narrow | Relatively broad |
| Diversity | High (63 species) | Moderate (22 species) |
| Sensitivity to perturbation | Extinction-prone | Relatively resistant |

gies are likely to evolve on each island. Indeed, some growth forms or ecological roles are clearly missing from certain islands. For example, subherbaceous treelets with pubescent leaves (e.g., *Cyanea degeneriana* and *C. pilosa*) that vegetatively mimic species of *Cyrtandra* (Gesneriaceae) are found exclusively on Maui and the island of Hawai'i.

A more satisfying explanation is available, however, for the great species richness of *Cyanea* relative to *Clermontia*. This disparity undoubtedly reflects ecological differences between the genera that shaped their evolution and that now expose them to quite different chances of extinction (Table 14.5).

Three differences seem crucial. First, *Cyanea* is a forest interior group, whereas *Clermontia* is a pioneer of forest gaps and edges. A branched growth habit allows *Clermontia* to respond opportunistically to unpredictable shifts in irradiance during early or gap-phase succession, whereas the unbranched form of *Cyanea* may be better suited to constant low light levels. It may be no accident that the only islands where there are large numbers of *Clermontia* species are Maui and Hawai'i, where frequent lava flows (and associated forest fires) now and in the recent past generated large amounts of early successional habitat. We suggest that *Clermontia* was far more common and diverse on older islands when they were several million years younger and that many species have become extinct with the loss of abundant, early successional habitats associated with volcanism at mid-elevations.

Second, the flowers of *Clermontia* are cut to the base of the corolla tube and so may have been visited by a broader range of honeycreepers and other pollinators than comparably sized *Cyanea* flowers. This difference accords with the early successional nature of the habitats occupied by most *Clermontia* and with the tendency for longer, more exclusionary bird-pollinated flowers to occur in more shaded sites, as discussed. A broader range of flower tube lengths in *Cyanea* is also consistent with a greater potential for reproductive isolation via the partitioning of nectarivores of widely differing bill lengths.

Finally, and most important, we believe that an understory group such as *Cyanea* had more limited powers of seed dispersal than that of a pioneer lineage such as *Clermontia* and that this difference has had a cascading series of effects on gene flow, extent of geographic and elevational ranges and tendency to speciate, species diversity within and among islands, and rates of extinction. We believe that *Cyanea* had lower powers of seed dispersal than *Clermontia* because their fruits were much smaller (and thus perhaps less attractive) and because *Cyanea* would have relied on forest interior birds to eat their fruits and disperse their seeds. On other islands, forest interior birds are relatively sedentary and less likely to cross water barriers and inappropriate habitat (Diamond et al., 1976). Presumably, this would have been true in the Hawaiian archipelago as well, but that is now impossible to ascertain. Little is known about avian frugivores in the Hawaiian Islands because they have been especially hard hit by extinction (Freed et al., 1987) or, as with most surviving members of the avifauna, greatly reduced in abundance and elevational range. Before the arrival of the Polynesians, frugivores would have included several species of honeycreepers, the Hawaiian Thrush and its relatives, the Hawaiian Crow and its relatives, and honeyeaters (Amadon, 1950; Freed et al., 1987; Olson and James, 1991).

Whether because of a dependence on forest interior birds or possession of less attractive fruit, a relatively low seed dispersal capacity in *Cyanea* would have reduced gene flow, increased geographic isolation, and fostered a high rate of speciation (Diamond et al., 1976). Reduced dispersal rates and high rates of speciation should, in turn, have resulted in narrower geographic and elevational ranges in *Cyanea* (and especially in the orange-fruited clade, even more strongly associated with forest interior conditions), due to differences in colonization rates and community packing. In fact, *Cyanea* does exhibit much narrower endemism than *Clermontia*: 89% of its species are restricted to single islands, compared with only 58% of *Clermontia* species. The average elevational range of

Cyanea species is 438 ± 294 m versus 840 ± 367 m for species of *Clermontia* ($P < .0001$, two-tailed t test, 59 d.f.).

Finally, the narrow geographic and elevational ranges of individual *Cyanea* species, their limited dispersal, and their usual dependence on a narrower range of pollinators may have made them more susceptible to extinction. In the face of the pressures wrought by widespread habitat destruction, decimation of lobelioid pollinators and dispersers, and introduction of alien mammalian browsers, 22% of all species of *Cyanea* (including *Rollandia*) are now extinct, and 29% are currently greatly endangered, often known from only one or two individuals (see Table 14.1). By comparison, only 5% of historically known species of *Clermontia* are extinct, and 13% are currently endangered (see Table 14.1). As we would predict from the foregoing, the principal factors correlated with the likelihood of a historically known species going extinct are initial rarity (Terborgh and Winter, 1980), occurrence in areas heavily disturbed by humans, and possession of longer, more specialized flowers.

Eight of the 14 extinct species were known historically from only one site, compared with only 4 of 49 extant species ($\chi^2 = 9.61$, $P < .01$ with 1 d.f.), including the just-described *Cyanea eleeleensis* and *C. kolekolenensis* and the recently rediscovered endangered *C. dunbarii* and *C. recta*. The average elevational range of the extinct species (to the extent data are available) is significantly less than that for extant species (182 m versus 481 m, $P < .01$, two-tailed t test with 38 d.f.). According to Rock (1919), the extinct species *C. arborea*, *C. comata*, *C. pohaku*, and *C. quercifolia* all occurred on leeward East Maui, in habitats that were heavily logged or cleared for pastures or *Eucalyptus* plantations; *C. giffardii* occurred on a single *kipuka* near Glenwood on Hawai'i that was largely cleared for cattle grazing. Finally, extinction has occurred at a significantly higher rate among species with longer flowers and is absent among species with a typical corolla tube length less than 45 mm (Table 14.6). It is not clear whether this is purely a result of the more-specialized pollination requirements of long-flowered species or whether the occurrence of many short-flowered species on Kaua'i, which has had less logging and grazing at middle elevations than other islands, has created this correlation as an artifact. The extinction rate of historically known species of *Cyanea* (including *Rollandia*) was highest on Maui (8 of 21 species, or 38%) and lowest on Kaua'i (none of the 16 species) and O'ahu (none of the 14 species). Thirteen of the 14 extinctions occurred in the *orange-fruited* clade, a higher rate (25%) than in the *purple-fruited* clade (7.7%),

TABLE 14.6. Corolla Tube Length of Extant and Extinct Species of *Cyanea*

| Corolla tube length (mm) | No. of species | |
|-----------------------------|----------------|---------|
| | Extant | Extinct |
| 15–29 | 10 | 0 |
| 30–44 | 13 | 0 |
| 45–59 | 4 | 7 |
| 60–74 | 7 | 5 |
| 75–89 | 2 | 1 |

$\chi^2 = 17.56$; $P < .002$, 4 d.f.
Data compiled from Lammers (1990a).

although the difference is not statistically significant ($P > .1$, χ^2 test with 1 d.f.).

The past extinction—and looming future loss—of large numbers of *Cyanea* species is of broad concern. Not only did this genus contribute 1 of every 15 plant species to the native flora and constitute one of the most widespread and characteristic elements of mesic and wet forest vegetation (Rock, 1919), it also played a starring role as a “keystone mutualist” (Gilbert, 1980; Terborgh, 1986) in helping create and maintain biological diversity in the Hawaiian biota.

Specifically, the evolution of *Cyanea* and other baccate lobelioids may have been interrelated with that of the avifauna that pollinated their flowers and dispersed their seeds. Lobelioids were particularly important, and *Cyanea* especially so, as nectar sources for birds with long bills and may have played a role in the evolution of the long-billed portions of the honeycreeper radiation. To the extent that *Cyanea* and other lobelioids provided a common nectar source for long-billed honeycreepers (e.g., *Drepanis*, *Hemignathus*, *Vestiaria*), they may have helped maintain not only those specialized nectarivores but also other plant groups that depend on their services (e.g., *Stenogyne* [20 species] of the Lamiaceae, *Hibiscadelphus* [6 species] of the Malvaceae), as well as the nectarivorous nitidulid beetles (Rock, 1919) frequently found in lobelioid flowers. Species of *Cyanea*, *Clermontia*, and *Rollandia* provide mating sites and food sources for many species of *Drosophila*, the most species-rich radiation of Hawaiian insects, and the best-studied example of insular evolution and speciation in the world (Carson, 1987b; Simon, 1987). They provided sites on which succinid snails grazed on epiphytic fungi and

algae (Carlquist, 1974). Finally, certain species of *Cyanea* may have helped shape the evolution of an extinct series of flightless geese and moa-nalos, the distinctive Hawaiian contingent of terrestrial browsers.

It is a disturbing fact that, even though the Hawaiian lobelioids—and especially *Cyanea*—provide some of the best material in the world for studies of plant evolution on islands, many of them today are in great peril of extinction. They have been driven to the very brink by habitat destruction, grazing by goats, pigs, and cattle, competition with exotic plants, and loss of many avian pollinators and seed dispersers. The efforts of the National Tropical Botanical Garden, The Nature Conservancy, and the National Park Service to protect these species deserve our strongest support. To save these plants, we must immediately implement an integrated program, involving (1) fencing of relict populations to protect them from herbivores; (2) protection of endangered species from logging on public and private lands; (3) establishment of saplings of each species at arboreta; (4) continued efforts to propagate species from seed and to obtain fruits of species that are rare or thought to be extinct; and (5) widespread implementation of new advances (by G. Koob, University of Hawaii) in the cloning of nonflowering individuals via tissue culture.

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E. Knox provided valuable information regarding the position of cpDNA rearrangements in Hawaiian lobelioids and supplied several penetrating comments on the manuscript and other aspects of lobelioid evolution. S. Downie and J. Palmer kindly supplied a series of precisely

mapped *Nicotiana* cpDNA clones. H. James and S. Olson provided several comments regarding the biology of the extinct Hawaiian avifauna and access to photographs and drawings of subfossil remains; M. Hadfield drew our attention to useful references on Hawaiian land snails. B. Baldwin, S. Carlquist, D. Crawford, V. Funk, P. Grant, H. Iltis, T. Lammers, E. Mayr, P. Soltis, and W. L. Wagner contributed valuable comments on an early draft. L. Mehrhoff provided useful information on the most recent rediscoveries by S. Perlman and J. Lau of *Cyanea* species previously thought to be extinct. We salute the heroic efforts of these and other intrepid Hawaiian botanists in scouring rugged terrain to find and help propagate endangered elements of the native flora.

APPENDIX 14.1. Presence/Absence of cpDNA Restriction Sites in the 32 Taxa Involved in the Study of Phylogenetic Relationships within *Cyanea* and *Rollandia* (see Figure 14.8)

Restriction site descriptors: 0, absent; 1, present; ?, unknown.

| Species | Restriction sites |
|-----------------------------------|--|
| (1) <i>Brighamia insignis</i> | 00101100110001101101000111111100000001100000010011100100010 |
| (2) <i>Clermontia arborescens</i> | 0011101010000010111100001110001010000111001000100001101000010 |
| (3) <i>Rollandia angustifolia</i> | 0010101101000001111000011100011010100001001100100001101110010 |
| (4) <i>Rollandia crispa</i> | 0010101101000001111000011100011010100001001100100001101110010 |
| (5) <i>Rollandia humboldtiana</i> | 0010101101000001111000011100011010100001001100100001101110010 |
| (6) <i>Rollandia lanceolata</i> | 0010101101000001111000011100011010100001001100100001101110010 |
| (7) <i>Rollandia longiflora</i> | 0000101101000001111000011100011010100001001100100001101110010 |
| (8) <i>Rollandia st-johnii</i> | 0010101101000001111000011100011010100001001100100001101110010 |
| (9) <i>Cyanea acuminata</i> | 0010101111000001111000011100011010100001001100100001101110000 |
| (10) <i>Cyanea grimesiana</i> | 0010101111000001111000011100011010100001001?00100001101110010 |
| (11) <i>Cyanea remyi</i> | 1010001111000001111000011100011010000001001100100001101110010 |
| (12) <i>Cyanea fissa</i> | 1010001111000001111000011100011010000001001100100001101110010 |
| (13) <i>Cyanea hirtella</i> | ????????????????????????????1100???????????????????????????????? |
| (14) <i>Cyanea sylvestris</i> | ????????????????????????????1100???????????????????????????????? |
| (15) <i>Cyanea undulata</i> | ????????????????????????????1100???????????????????????????????? |
| (16) <i>Cyanea lobata</i> | 0010001111001001011000011100011010001001011100100001101110010 |
| (17) <i>Cyanea scabra</i> | 0010001111000001111000011100011010001001011100100001101110010 |
| (18) <i>Cyanea tritomantha</i> | 0010001111000001111000011100011010001001011100100001101110010 |
| (19) <i>Cyanea solanacea</i> | 0010001111000001111000011000010010001001001100100001101110010 |
| (20) <i>Cyanea aculeatiflora</i> | 0010101111100001111000011100011010000001001100100001101110010 |
| (21) <i>Cyanea macrostegia</i> | 0010101111100001111000011100011010000001001100100001101110010 |
| (22) <i>Cyanea copelandii</i> | 0010101111000001111010011100011010000001001100100001101110010 |
| (23) <i>Cyanea pilosa</i> | 0010101111000001111000011100011010000001001100100001101110010 |
| (24) <i>Cyanea hardyi</i> | 0110101011000000101000110100011111000000001?00101100011111011 |
| (25) <i>Cyanea spathulata</i> | 01101010110000001010001101000111110000000010001011000?1111111 |
| (26) <i>Cyanea angustifolia</i> | 0110101011010000101000110100011111000000001000101100011111011 |
| (27) <i>Cyanea coriacea</i> | ????????????????????????????1110???????????????????????????????? |
| (28) <i>Cyanea membranacea</i> | 0110101011000000111000011100011111010000101000101100111111011 |
| (29) <i>Cyanea hamatiflora</i> | 0110101011000000111001011100011111000000001010101100111111011 |
| (30) <i>Cyanea mannii</i> | 0110101011000000111000011100011111000000001001101100111111011 |
| (31) <i>Cyanea elliptica</i> | 0110101011000000111000011100011111000000001001101100111111011 |
| (32) <i>Cyanea leptostegia</i> | 0110101011000000111000011100011111000000001?0010110011111?011 |

APPENDIX 14.1 (Extended)

| Species | Restriction sites |
|---------|---|
| (1) | 000011000001011111000011001011000111001101111110000110000001010011001101101100000010010 |
| (2) | 000011000000110110000010011010101010001101110011110110101111010010000101100111010000100 |
| (3) | 0000110010000100100000000110110010010110001010110100010111011010010001101100110010010110 |
| (4) | 0000110010000100100000000110110010010110001010110100010111011010010001100100110010010110 |
| (5) | 0000110010000100100000000110110010010110001010110100010111011010010001101100110010010110 |
| (6) | 0000110010000100100000000110110010010110001010110100010111011010010001101100110010010110 |
| (7) | 0000110010000100100000000110110010010110001010110100010111011010010001101100110010010110 |
| (8) | 0000110010000100100000000110110010010110001010110100010111011010010001101100110010010110 |
| (9) | 0000010000000100100000000110110010011110001110110100010111011010010001101100110010010110 |
| (10) | 0000110000000100100000000110110010010110001110110100010111011010010001101100110010010110 |
| (11) | 0000110000000100100000000110110010010110001110110101010111011010010001001100110110011110 |
| (12) | 0000110000000100100000000110110010010110001110110101010111011010010001001100110110011110 |
| (13) | ????????????????????????????????10010110001110110100010111011010010001001100110111011111 |
| (14) | ????????????????????????????????10010110001110110100010111011010010001001100110111011111 |
| (15) | ????????????????????????????????10010110001110110100010111011010010001001100110111011111 |
| (16) | 0000110000000100100000000110110010010110001110100100010111011010010001101100110010010110 |
| (17) | 0000110000000100100000000110110010010110001110100100010111011010010001101100110010010110 |
| (18) | 0000110000000100100010000110110010010110001110100100010111011010010001101100110010010110 |
| (19) | 0000110000000100100000000110110010010110001110110100010111011010000001101100110010010110 |
| (20) | 0000110000000000100000000110110010010110001100110100011111011010110001101000110010010110 |
| (21) | 0000110000000000100000000110110010010110001100110100010111011010110001101000110010010110 |
| (22) | 0000111000100100100000000110110010010110001110110100010111011010110001101000110010010110 |
| (23) | 0000110000000100100000000110110010010110001110110100010111011010110001101000110010010110 |
| (24) | 1011110101000001101001001101010010110011010111110100111101011001010101111100010010110110 |
| (25) | 1011110101000001101001001101010010110011010111110100111101011001010101111100010010110110 |
| (26) | 0011110101000001101001001101010010110011011111110100111101011000010101111100110010110110 |
| (27) | ????????????00101100001000111010010110011011111110100110101011000010001111100110010110110 |
| (28) | 0011100101000101100101000111010110110011011111110100110101010110010011101110110010010110 |
| (29) | 0011110101000101100101000111010110110001011111110100100101010010010011101110110010010110 |
| (30) | 0011110101000101100101000111010010110011111111110100110101011010010011101110110010010110 |
| (31) | 0011110101000101000101000111010010110011111111110100110101011010010011101110110010010110 |
| (32) | 0111110101000101100101000111010010110011011111110100110101010010010001101100110010010110 |

15

Patterns of Speciation and Biogeography in *Clermontia* (Campanulaceae, Lobelioideae)

THOMAS G. LAMMERS

Clermontia (Campanulaceae, Lobelioideae) is a genus of trees and shrubs endemic to the Hawaiian archipelago. It is distinguished from other genera in the subfamily by its repeatedly branched and spreading woody stems, axillary few-flowered inflorescences, corolla cleft dorsally to near the base, and large thick-walled orange or yellow berries (Rock, 1919; Wimmer, 1943; Lammers, 1991). The woodiness, axillary inflorescences, and baccate fruit are unusual characters among Lobelioideae. Only two other genera, also Hawaiian endemics, share this unique suite of features: *Cyanea* (including *Rollandia*, cf. Lammers et al., 1993) and *Delissea* (Lammers, 1990a). Together, these three genera compose the subtribe Cyaneinae of the tribe Delisseeae (Wimmer, 1943).

Clermontia (Figure 15.1) includes 22 species and 9 heteronymic subspecies (Table 15.1), making it the sixth largest of the 216 flowering plant genera indigenous to the Hawaiian Islands (Wagner et al., 1990) and the seventh largest of the 30 genera in the subfamily (Lammers, 1993). The genus is remarkably homogeneous in vegetative features, and nearly all taxonomically useful variation involves the flowers. Six series are recognized (Lammers, 1991) on the basis of differences in various structural features of the corolla (curvature of the tube and arrangement, posture, and relative length of the lobes) and staminal column (exsertion). The series are grouped into two sections on the basis of features of the calyx lobes (relative length, shape, texture, persistence, fusion, and color). Each series thus constitutes a group of species in which the flowers have



FIGURE 15.1. *Clermontia montis-loa* (section *Clermontia*), showing the petaloid calyx lobes characteristic of that section. Photograph taken by the author on September 4, 1983, near the Wailuku River on the windward slopes of Mauna Kea, Hawai'i, and documented by *Lammers* 5425 (B, BISH, F, OS, PH).

the same general form and configuration, but that vary in presentation (pendent, horizontal, erect), color (from pure white to almost black), or various quantitative features (e.g., diameter of corolla tube, width of corolla lobes, length of staminal column).

In the series assigned to section *Clermontioideae*, the calyx lobes, like those of most other Lobelioideae, are not petaloid: less than half the length of the corolla, distinct, persistent, more or less triangular, green, and firm. In series *Clermontioideae*, the corolla is bilabiate, with the lobes spreading and as long as or longer than the suberect or curved tube; the staminal column may be included or exserted. In series *Sarcanthae*, the corolla is bilabiate with thick, fleshy, erect, or slightly spreading lobes (the two dorsal longer than the three ventral), and the staminal column is included. In series *Unilabiatae*, the corolla is unilabiate, with lobes one-fifth to one-quarter as long as the curved or arcuate tube; the staminal column is strongly exserted.

In section *Clermontia*, however, the calyx lobes are petaloid, as long as the corolla (rarely as little as two-thirds its length), basally connate for

TABLE 15.1. Synopsis of the Classification of *Clermontia*, with Information on the Geographic Distribution and Elevational Range of Each Species and Subspecies

| Taxon (abbreviation ^a) | Distribution ^b | Elevation (m) |
|---|---|---------------|
| Section <i>Clermontioideae</i> | | |
| Series <i>Clermontioideae</i> | | |
| <i>C. clermontioides</i> (Gaud.) A. Heller (CLE) | | |
| subsp. <i>clermontioides</i> | H _L | 670–1,525 |
| subsp. <i>rockiana</i> (E. Wimm.) Lammers | H _L | 840–1,825 |
| <i>C. pyrularia</i> Hillebr. (PYR) | H _W , H _L | 1,585–2,130 |
| <i>C. waimeae</i> Rock (WAI) | H _K | 1,070–1,520 |
| Series <i>Sarcanthae</i> | | |
| <i>C. arborescens</i> (H. Mann) Hillebr. (ARB) | | |
| subsp. <i>waikoluensis</i> (St. John) Lammers | Mo, L | 520–1,280 |
| subsp. <i>waihia</i> (Wawra) Lammers | M _W , M _E | 610–1,825 |
| subsp. <i>arborescens</i> | M _W | 550–1,325 |
| <i>C. tuberculata</i> C. Forbes (TUB) | M _E | 1,650–1,825 |
| Series <i>Unilabiatae</i> | | |
| <i>C. peleana</i> | | |
| subsp. <i>singuliflora</i> (Rock) Lammers (PEL _S) | M _E , H _W | ? |
| subsp. <i>peleana</i> (PEL _P) | H _W | 530–1,150 |
| <i>C. fauriei</i> H. Lév. (FAU) | K, O _W , O _K | 365–1,400 |
| Section <i>Clermontia</i> | | |
| Series <i>Kakeanae</i> | | |
| <i>C. kakeana</i> Meyen (KAK) | O _W , O _K , Mo, M _W , M _E | 120–1,270 |
| <i>C. lindseyana</i> Rock (LIN) | M _E , H _W , H _L | 1,220–1,825 |
| <i>C. persicifolia</i> Gaud. (PER) | O _W , O _K | 300–850 |
| <i>C. pallida</i> Hillebr. (PAL) | Mo | 915–1,390 |
| <i>C. kohalae</i> Rock (KOH) | H _K , H _W | 370–1,370 |
| <i>C. montis-loa</i> Rock (MON) | H _W | 1,070–1,700 |
| <i>C. drepanomorpha</i> Rock (DRE) | H _K | 915–1,460 |
| Series <i>Parviflorae</i> | | |
| <i>C. multiflora</i> Hillebr. (MUL) | O _K , M _W | ? |
| <i>C. micrantha</i> (Hillebr.) Rock (MIC) | L, M _W | 670–1,460 |
| <i>C. parviflora</i> Gaud. ex A. Gray (PAR) | H _K , H _W | 120–1,460 |
| <i>C. calophylla</i> E. Wimm. (CAL) | H _K | 885–1,460 |
| Series <i>Clermontia</i> | | |
| <i>C. oblongifolia</i> Gaud. | | |
| subsp. <i>oblongifolia</i> (OBL _O) | O _W , O _K | 395–1,200 |
| subsp. <i>mauiensis</i> (Rock) Lammers (OBL _M , p.p.) | L, M _W , M _E | 800–990 |
| subsp. <i>brevipes</i> (E. Wimm.) Lammers (OBL _M , p.p.) | Mo | 1,220–1,280 |
| <i>C. grandiflora</i> Gaud. (GRA) | | |
| subsp. <i>munroi</i> (St. John) Lammers | Mo, L, M _W , M _E | 525–1,975 |
| subsp. <i>grandiflora</i> | M _W | 610–1,750 |
| subsp. <i>maxima</i> Lammers | M _E | 1,640 |
| <i>C. samuelii</i> C. Forbes (SAM) | | |
| subsp. <i>hanaensis</i> (St. John) Lammers | M _E | 610–1,860 |
| subsp. <i>samuelii</i> | M _E | 1,675–2,100 |
| <i>C. hawaiiensis</i> (Hillebr.) Rock (HAW) | H _L | 550–1,760 |

^ap.p. indicates pro parte.
^bK, Kaua'i; O_W, O'ahu, Wai'anae Mts.; O_K, O'ahu, Ko'olau Mts.; Mo, Moloka'i; L, Lana'i; M_W, West Maui; M_E, East Maui; H_K, Hawai'i, Kohala Mts., H_W, Hawai'i, Mauna Kea and windward Mauna Loa; H_L, Hawai'i, Hualalai and leeward Mauna Loa.

TABLE 15.2. Distribution of the Species of *Clermontia* by Island, with Information on Maximum Age, Area, and Maximum Elevation of Each Island

| Island | Maximum age (millions of years) ^a | Area (km ²) ^a | Maximum elevation (m) ^a | <i>Clermontia</i> spp. | | |
|----------|--|---|--|------------------------|--------------------|--------------|
| | | | | Total species | Endemic species | % Endemic |
| Kaua'i | 5.72 | 890 | 1,573 | 1 | 0 | 0 |
| O'ahu | 3.8 | 979 | 1,208 | 5 | 1 | 20 |
| Moloka'i | 1.84 | 420 | 1,491 | 5 | 1 | 20 |
| Lana'i | 1.46 | 225 | 1,011 | 4 | 0 | 0 |
| Maui | 1.63 | 1,174 | 3,007 | 10 | 2 | 20 |
| Hawai'i | 0.7 | 6,501 | 4,139 | 11 | 9 | 82 |

^aData from Macdonald et al. (1983).

one-fifth to four-fifths their length (dorsal lobe distinct nearly to base), deciduous with the corolla, and matching it in shape, color, and texture. This creates a “double-flowered” perianth that is unique in the family. In series *Clermontia*, the perianth is essentially tubular, with suberect or slightly spreading lobes one-fifth to one-half as long as the curved or arcuate tube; the staminal column is included or slightly exserted. In series *Kakeanae*, the perianth is bilabiate, with the lobes spreading and as long as or longer than the suberect or gently curved tube; the staminal column is included or slightly exserted. In series *Parviflorae*, the perianth is rotate with strongly recurved lobes as long as or longer than the erect or suberect tube; the staminal column is strongly exserted.

Several interesting patterns are seen in the geographic distribution of *Clermontia* (Tables 15.1 and 15.2; Figure 15.2). As expected on the basis of island biogeographic theory (MacArthur and Wilson, 1967), there is a general increase in number of species as one proceeds from small islands to large and from low islands to high. Contrary to expectations, however, the number of species decreases as one proceeds from younger to older islands. The youngest island, Hawai'i, is home to 11 species, whereas Kaua'i, the oldest main island, has but 1. Kaua'i also has far fewer species than one would expect based on its size and elevation.

Most of the species (59%) are endemic to a single island. In many cases, these single-island endemics actually are even more narrowly restricted (e.g., *Clermontia calophylla* and *C. drepanomorpha* to the Kohala Mountains of northwestern Hawai'i and *C. samuelii* to the Hana District of East Maui). The island with the highest levels of endemism by far is Hawai'i. Nine (69%) of the single-island endemics occur there.

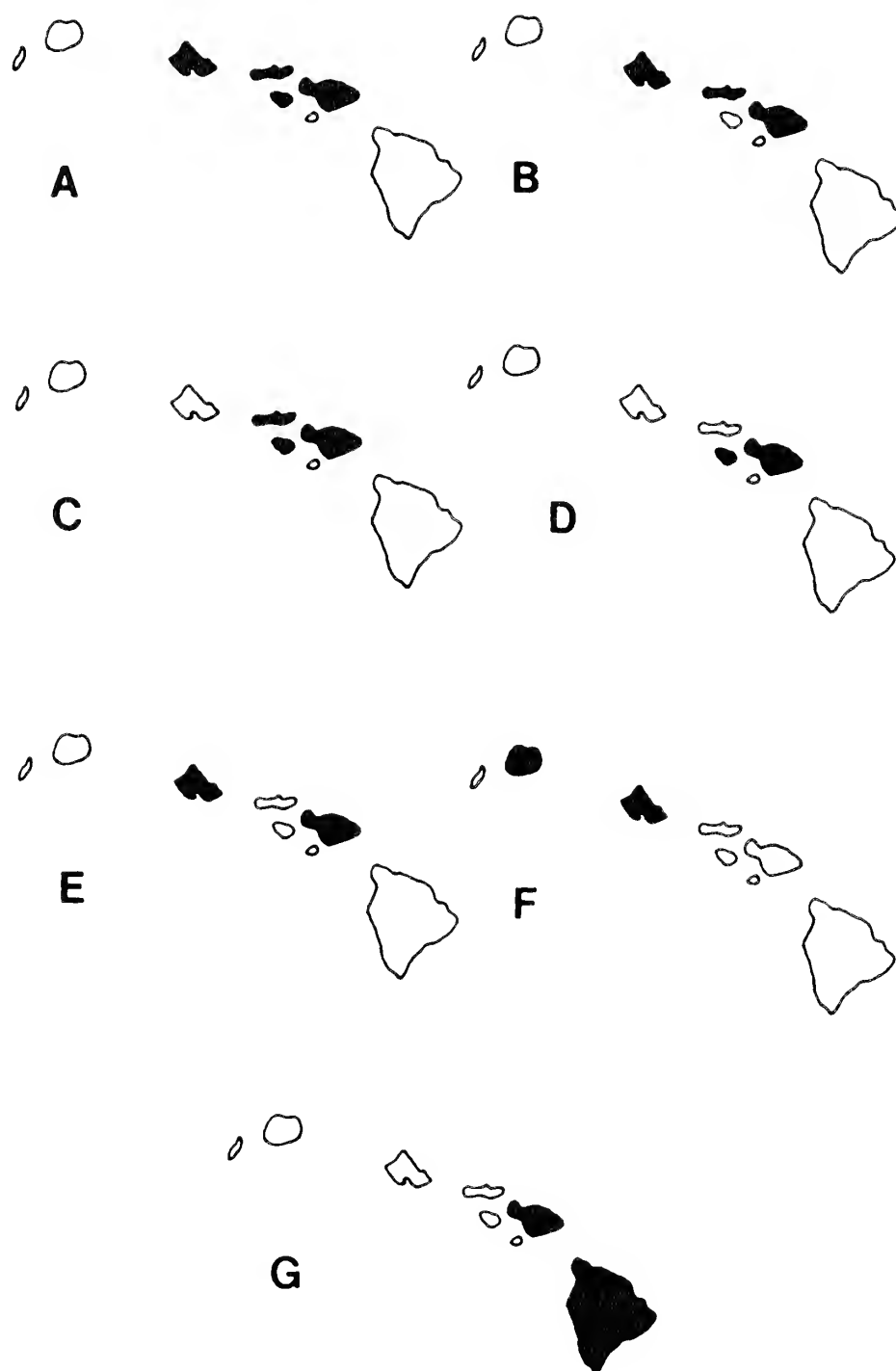


FIGURE 15.2. Patterns of geographic distribution in species of *Clermontia* occurring on more than one island (*filled-in island*). (A) O'ahu-Moloka'i-Lana'i-Maui (*C. oblongifolia*); (B) O'ahu-Moloka'i-Maui (*C. kakeana*); (C) Moloka'i-Lana'i-Maui (*C. arborescens*, *C. grandiflora*); (D) Lana'i-Maui (*C. micrantha*); (E) O'ahu-Maui (*C. multiflora*); (F) Kaua'i-O'ahu (*C. fauriei*); (G) Maui-Hawai'i (*C. lindseyana*, *C. peleana*).

These nine species represent 82% of the species of *Clermontia* found on that island (Table 15.2).

Although the genus is represented on all six of the high islands in the archipelago, no one species occurs on all six (see Table 15.1; Figure 15.2). The most widely distributed species is *Clermontia oblongifolia*, found on

the four central islands (O‘ahu, Moloka‘i, Lana‘i, and Maui) (Figure 15.2A). Five species have distributions that represent subsets of these four islands: *C. kakeana* (O‘ahu, Moloka‘i, and Maui) (Figure 15.2B); *C. arborescens* and *C. grandiflora* (Moloka‘i, Lana‘i, and Maui) (Figure 15.2C); *C. micrantha* (Lana‘i and Maui) (Figure 15.2D); and the extinct *C. multiflora*, known from single collections on O‘ahu and Maui (Figure 15.2E). The sole species on Kaua‘i, *C. fauriei*, also occurs on O‘ahu (Figure 15.2F), and two species found on Hawai‘i, *C. lindseyana* and *C. peleana*, also occur on Maui (Figure 15.2G). Overall, one species is known from four islands (Figure 15.2A), three species from three islands (Figures 15.2B and C), and five species from two islands (Figures 15.2F and G).

Four of the five two-island species are very nearly single-island endemics, as each is much more common on one island than on the other. For example, I have seen nearly 90 collections of *Clermontia fauriei* from Kaua‘i but only 4 from O‘ahu; similarly, 38 specimens of *C. micrantha* from Maui have been examined but only 3 from Lana‘i (Lammers, 1991). In fact, the two species common to Maui and Hawai‘i, *C. lindseyana* and *C. peleana*, were thought to be endemic to Hawai‘i until quite recently, because the few specimens from East Maui had long been misidentified as *C. kakeana* and *C. fauriei*, respectively (Lammers, 1991). The sole exception to this pattern is the extinct *C. multiflora*, whose existence on O‘ahu and Maui is documented by a single collection from each. This is also the only one of the nine multi-island species that is known from nonadjacent islands (Figure 15.2E). Given the early date of extinction of this species (before 1871) (Lammers, 1991), the observed distribution could be the result of the extinction of populations on intervening islands rather than an actual case of “leapfrog” dispersal. Conceivably, this species once may have had a more extensive range in the central islands, similar to that of *C. oblongifolia* (Figure 15.2A) or *C. kakeana* (Figure 15.2B).

Although the distributional data indicate considerable geographic overlap among species of *Clermontia*, sympatric species typically are not closely related. For example, four species occur in mid-elevation forests on windward Hawai‘i. However, each belongs to a different taxonomic series: *C. hawaiiensis* to series *Clermontia*, *C. montis-loa* to series *Kakeanae*, *C. parviflora* to series *Parviflorae*, and *C. peleana* to series *Unilabiatae*. As a result, the species of *Clermontia* in a given area typically possess flowers of different structural types. In the few cases involving sympatry of close relatives, the flowers typically exhibit pronounced differences in color or size. For example, *C. kakeana* and *C. persicifolia*

of series *Kakeanae* are sympatric in the Ko'olau Mountains of O'ahu; the former has a green perianth and relatively short magenta staminal column, and the latter has a white perianth and longer white staminal column.

Clermontia is restricted to the lowland and montane zones (Gagné and Cuddihy, 1990). Populations are most commonly found between 500 and 1,500 m (see Table 15.1). Some species ascend as high as 2,130 m in the mountains, but only four taxa (*C. grandiflora* subsp. *maxima*, *C. pyrularia*, *C. samuelii* subsp. *samuelii*, and *C. tuberculata*) are restricted to elevations above 1,500 m. A few species descend to 120 m in places, but none is restricted to sites below 500 m. Most species occur in mesic to wet forests and in wet shrublands (Gagné and Cuddihy, 1990); *C. drepanomorpha*, *C. grandiflora* subsp. *grandiflora*, and *C. micrantha* are found in montane bogs. Populations in forest communities generally grow in rather open sites (e.g., forest margins, canopy gaps, windfalls, ridge crests) rather than under a dense canopy. Most species are facultatively epiphytic, with shrubs and even small trees growing on the bryophyte-covered trunks and upper branches of larger trees.

Flowers of *Clermontia*, like those of most Campanulaceae, are strongly protandrous, an indication that outcrossing (xenogamy) may be the predominant breeding system (Bertin and Newman, 1993). Several lines of evidence point to endemic nectar-feeding passerine birds as the most likely pollen vectors. First, the ornithological literature contains many reports of such birds visiting flowers of *Clermontia* (Lammers and Freeman, 1986). The birds involved include endemic species of both Hawaiian honeycreepers (Drepanidinae) and honeyeaters (Meliphagidae). Second, the flowers exhibit the typical suite of morphological features associated with ornithophily (Stiles, 1978; Faegri and van der Pijl, 1979): deep, wide, heavy, tubular corollas, with abundant sequestered nectar and no odor, disposed in relatively few, large, long-lived inflorescences. Third, the floral nectar produced by species of *Clermontia* consists almost entirely of hexose sugars, with very little or no sucrose (Lammers and Freeman, 1986); plants pollinated by nectarivorous passerines characteristically produce this type of nectar (Baker and Baker, 1983). Fourth, pollen of Lobelioideae has been recovered in significant quantities from a museum skin of a Hawaiian honeycreeper (T. G. Lammers, unpubl.). This specimen (Bishop Museum 3379) was a male 'I'iwi (*Vestiaria coccinea*) collected on Maui in 1901. Despite their protandry, at least some species of *Clermontia* are capable of self-pollination (autogamy). In a series of

pollinator exclusion experiments involving *C. kakeana*, Cory (1984) demonstrated nearly 100% seed set in bagged flowers, as well as in the unmanipulated and hand-pollinated controls.

Birds may also function as seed dispersers for *Clermontia*. Various frugivorous species have been observed feeding on the berries, a fact reflected in the Hawaiian name for *C. fauriei*: *haha'aiakamanu* or "bird-food lobelioid" (Rock, 1919; Lammers, 1991). In particular, the 'O'u (*Psittirostra psittacea*) is known to have fed preferentially on the berries of *Clermontia* (Perkins, 1903; Munro, 1944).

Over the past 1,500 years, the Hawaiian avifauna has changed greatly, due to massive extinctions and range reductions among natives and the invasion and establishment of many aliens (Berger, 1981; Olson and James, 1982b). At least one of these alien birds, the Japanese White-eye (*Zosterops japonica*) has been observed visiting flowers of *Clermontia* (Lammers et al., 1987). As a result of these faunal changes, current rates of outcrossing and dispersal in species of *Clermontia* may differ significantly from rates before colonization of the archipelago by humans. The long-term biological consequences of such shifts are problematic.

MATERIALS AND METHODS

All 22 species of *Clermontia* were used as operational taxonomic units (OTUs) in the cladistic analyses. Also, two of these species were further divided into two OTUs each, because their constituent subspecies differ by one of the characters used here (Appendix 15.1). Within *C. oblongifolia*, subspecies *oblongifolia* differs from subspecies *mauiensis* and *brevipes* in character 5, petiole length. Within *C. peleana*, subspecies *peleana* and *singuliflora* differ in character 27, internal color of the corolla. This gives 24 OTUs in the ingroup.

It would have been most appropriate to have used the remainder of the Cyaneinae (*Cyanea* and *Delissea*) as the outgroup. However, this proved wholly impractical. Many characters that vary within *Clermontia* also vary within these genera (e.g., petiole length, peduncle length, hypanthium shape, staminal column exsertion). Eliminating them would have reduced the number of usable characters to less than the number of OTUs. As a result, it was necessary to select some subset of the Cyaneinae to use as an outgroup to have an adequate number of characters.

The outgroup chosen comprised two members of *Cyanea* section *Hirtellae* (Lammers, 1992), *C. hirtella* (H. Mann) Hillebr. and *C. sylvestris* A. Heller. These two species, both endemic to Kaua'i (Lammers, 1990a), were identified previously (Lammers, 1991) as the species most similar to *Clermontia*. Among the potential synapomorphies supporting this relationship are stem branching patterns, facultative epiphytism, inflorescence type, floral size, and fruit color (Lammers, 1991). As these two species do not differ in any character used in the cladistic analyses, they were treated as a single OTU.

Thirty-two morphological characters, representing both vegetative and floral features, were selected (Appendix 15.1). Given the size of the ingroup, this is a relatively small number of characters. Unfortunately, most of the characters that are useful taxonomically in *Clermontia* are quantitative and continuous. Cladistic methods, particularly computer-implemented ones, work best when the characters can be divided into two discrete and mutually exclusive states (Chappill, 1989). Thus, many characters of great importance in the classification of the genus perforce were eliminated from the analyses.

Each character was divided into two or, less often, three states (see Appendix 15.1). All the tristate characters were treated as unordered, except character 6, the number of flowers per peduncle, which was treated as a linear reduction series. State changes were polarized via comparison to the outgroup (Watrous and Wheeler, 1981).

The basic data matrix (Appendix 15.2) was analyzed using PAUP version 2.4 (Swofford, 1985). Trees were constructed by adding OTUs according to the CLOSEST algorithm. The MULPARS option was used to find multiple equally parsimonious trees. To find even shorter trees, branch swapping was effected using the SWAP=GLOBAL option; the large size of the data matrix precluded use of the more rigorous BANDB (branch-and-bound) algorithm (Hendy and Penny, 1982).

The resulting phylogenetic tree (Figure 15.3) was used to generate an area cladogram (Figure 15.4) by adding information on geographic distribution (Table 15.1). Because of the complex distributions of certain species (see Figure 15.2), the three youngest and most proximate of the central islands (Moloka'i, Lana'i, and Maui) will often be discussed collectively as the Maui Nui complex. More precise distributions within this complex are indicated in the discussion and given in Table 15.1. The phylogenetic tree also was superimposed on a generalized map of the archipelago, to yield a more schematic depiction of patterns of inter-island colonization and diversification (Figure 15.5).

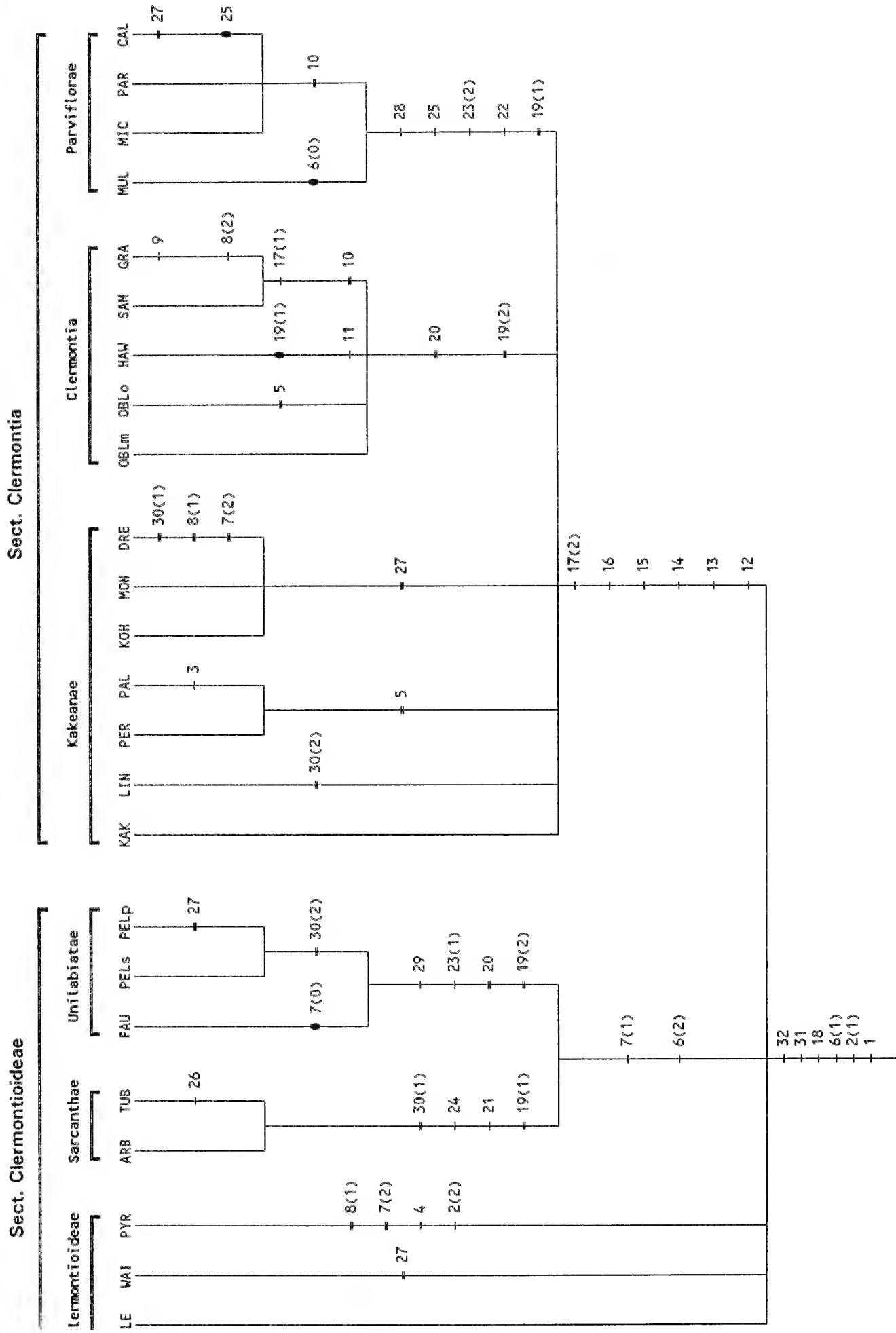


FIGURE 15.3. Cladogram for *Clermontia*. OTUs are identified by the abbreviations given in Table 15.1, and characters by the numbers given in Appendix 15.1. For tristate characters, the character state number is given parenthetically. Symbols: -, synapomorphy; =, parallelism; ●, reversal.

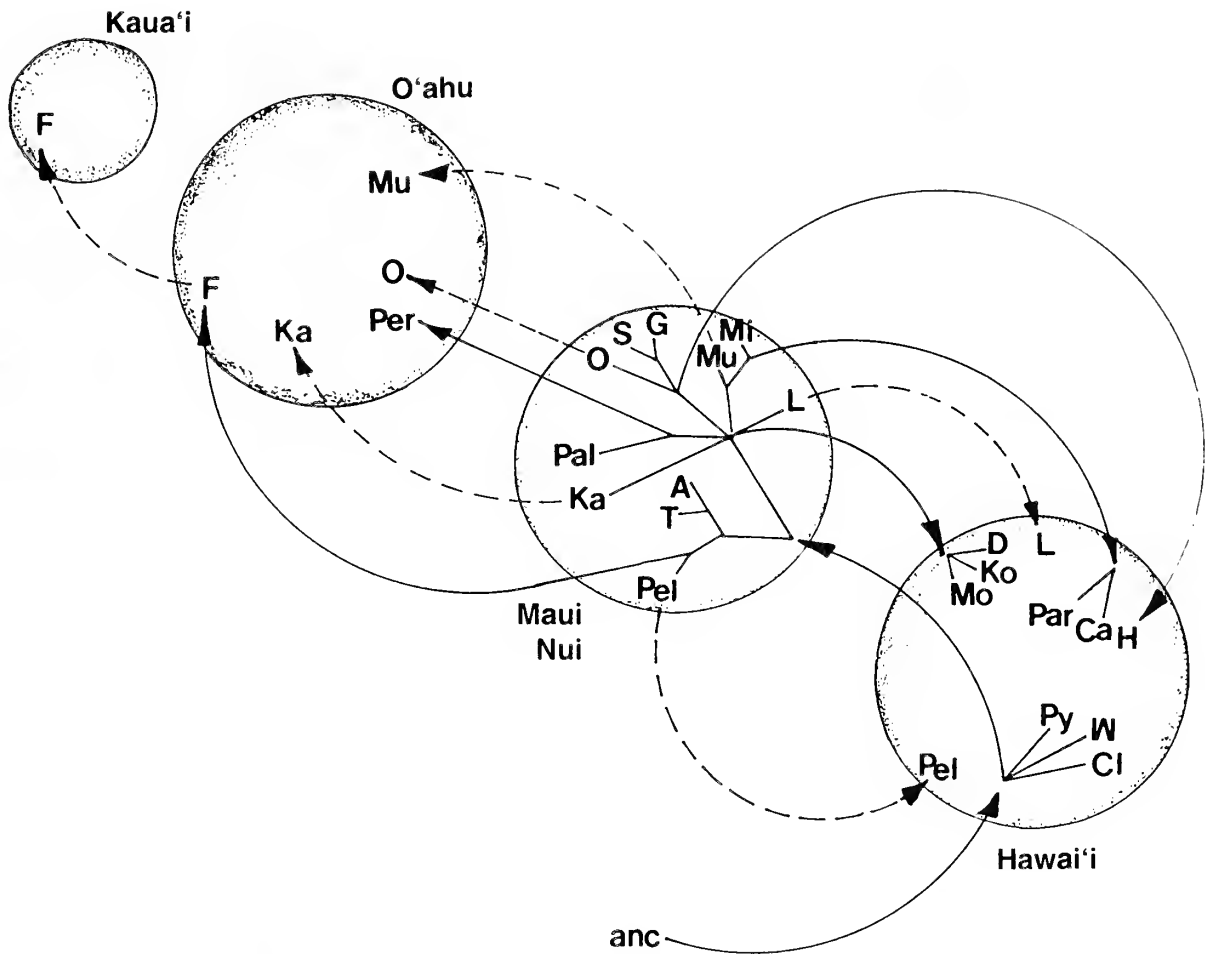


FIGURE 15.5. Schematic representation of the diversification and spread of *Clermontia* in the Hawaiian archipelago. Species are denoted by the first one, two, or three letters (as necessary to discriminate) of their specific epithet. Symbols: —, speciation within an island; →, speciation accompanying inter-island dispersal; - - →, inter-island dispersal unaccompanied by speciation.

RESULTS

Because of the relative paucity of characters that could be used in these analyses (see above), it was not possible for PAUP to fully resolve the phylogeny of *Clermontia*. More than 100 equally parsimonious trees were located. However, all of them were essentially identical, differing only in how the many polytomies were converted into series of dichotomies. The tree in Figure 15.3 represents the common topology underlying all these trees. It was constructed by collapsing all unsupported branches, thus reconstituting the polytomies. Resolution of this cladogram involved 56 character state changes. Of these, 22 were parallelisms and 4 were reversals, resulting in approximately 46% homoplasy; 7 state changes were uninformative (i.e., autapomorphies). The consistency index (CI) was 0.720.

Despite the high levels of homoplasy, it was possible to resolve some well-defined clades. The monophyly of the genus as a whole is supported by six synapomorphies involving habit, leaves, inflorescences, corolla, and fruits. The monophyly of section *Clermontia* is supported by six synapomorphies involving the calyx lobes. Four of the six taxonomic series are monophyletic: *Sarcanthae* and *Unilabiatae* in section *Clermontioideae*, *Parviflorae* and the autonymic series in section *Clermontia*. Further, the *Sarcanthae* and *Unilabiatae* together form a clade, which has not been accorded a formal name. Whether the remaining supraspecific taxa (section *Clermontioideae*, series *Clermontioideae*, and series *Kakeanae*) are monophyletic or paraphyletic is unresolved; such taxa may be described as metaphyletic (Kluge, 1989).

Although the large number of parallelisms is somewhat troubling, at least some of them appear to be genuine parallel developments of derived features rather than unrecognized synapomorphies. For example, *Clermontia drepanomorpha* and *C. pyrularia*, both of which are endemic to Hawai'i, share a unique inflorescence, in which the peduncle is declinate (character 8, state 1) and three to five times as long as the abruptly upcurved pedicels (character 7, state 2). However, these two species belong to different taxonomic sections and have no other apomorphies in common, aside from those that define the genus. Similarly, very dark purple ("black") floral pigmentation (character 27, state 1) has developed in four different taxonomic series: *Clermontioideae* (*C. waimeae*); *Kakeanae* (*C. drepanomorpha*, *C. kohalae*, *C. montis-loa*); *Parviflorae* (*C. calophylla*); and *Unilabiatae* (*C. peleana* subsp. *peleana*).

DISCUSSION

The discussion that follows is based strictly on two sets of data, the inferred phylogenetic tree (see Figure 15.3) and the known geographic distribution of the species (see Table 15.1), which were combined to produce an area cladogram (Figures 15.4 and 15.5). The many polytomies and parallelisms naturally cast doubt on how closely the tree represents actual patterns of evolutionary diversification in the genus. Although one might wish for a better resolved cladogram with less homoplasy, Figure 15.3 is the best tree that can be constructed at the present time on the basis of morphological data. As such, the biogeographic hypotheses outlined below must be predicated on it. The approach taken here has been to ask: If indeed the inferred tree is a

reasonable representation of the phylogenetic component of diversification, what does it tell us about the geographic component? If subsequent data fail to support the phylogenetic hypotheses embodied in the tree, the biogeographic hypotheses will also require revision.

It also has been necessary to assume that our understanding of the geographic distribution of *Clermontia* is relatively complete and accurate (i.e., that species have not been extirpated from an island without our knowledge). For example, if *C. persicifolia* is known only from O'ahu, then that is the only island it has ever occurred on. However, we know that many plants and animals endemic to the Hawaiian Islands have gone extinct or suffered range reductions since the arrival of humans in the archipelago (Kirch, 1982; Olson and James, 1982b; Wagner et al., 1985). Among the endemic Lobelioideae, fully 25% of the species have succumbed in historical times (Lammers, 1990a). Certainly, it may be speculated that, for example, *C. multiflora* once grew on Moloka'i or Kaua'i or even French Frigate Shoals. But doing so only multiplies biogeographic hypotheses endlessly, while reducing the degree of confidence to zero. The only productive and meaningful approach is to generate hypotheses on the basis of substantiated data and to alter or reject the hypotheses if and when new data become available.

In the absence of other data, one would assume that the island on which the basal lineage is found represents the island on which the group originated. Because the ages of the islands have been estimated via potassium-argon dating (Table 15.2), it is possible also to hypothesize the maximum time of divergence. In *Clermontia*, however, the lack of resolution at the base of the cladogram makes it very difficult to do so with any degree of confidence. In the absence of other data, it does not seem unreasonable to assume that the OTU that has changed least from its ancestor (i.e., that has the fewest apomorphies) might represent the basal lineage. Certainly, the clade formed by section *Clermontia* can be excluded from consideration as the basal lineage; the petaloid calyx that defines it is unique in the entire family.

The OTUs with the fewest apomorphies are the three species of series *Clermontioideae*: *Clermontia clermontioides* (no apomorphies), *C. waimeae* (one parallelism), and *C. pyrularia* (two parallelisms and two autapomorphies). All three are endemic to Hawai'i, the very youngest island of the chain. The oldest portion of this island, the Kohala volcano, appeared above the surface of the sea approximately 700 thousand years ago (ka); the portion of the island on which the most plesiomorphic

species (*C. clermontioides*) occurs arose only 500 ka (Macdonald et al., 1983).

Taken at face value, this would seem to suggest a very recent time of origin for *Clermontia*. However, several factors suggest caution in accepting this hypothesis. First, it runs counter to the pattern seen in most other Hawaiian angiosperms, in which the data suggest origins on older islands of the chain (see Funk and Wagner, this volume, Chapter 17). Second, a point of origin on Hawai'i is at the maximum possible geographic distance from the outgroup on Kaua'i. One would expect dispersal to be most frequent among adjacent islands. Third, an origin on Hawai'i would necessitate a large number of back-migrations (i.e., dispersals from a younger to an older island) and leave little time for them. The biota of an older island typically is more stable, with fewer open niches, and thus more difficult to colonize.

However, a relatively recent origin on Hawai'i might explain the paucity of species on Kaua'i and the peculiar concentration of species on the youngest islands of the chain. If *Clermontia* diverged on the youngest island, then the length of time that an island has been occupied by the genus would indeed run counter to the age of the island, as does the number of species per island. However, the expected relationship between the length of time that a lineage has been on an island and the number of species in that lineage would still result (i.e., the islands inhabited longest by a lineage would accumulate the most species). Presumably, the genus reached Kaua'i only recently; despite that island's size and physiographic diversity, there simply may not have been sufficient time for the genus to diversify there. The paucity of open niches on an old, ecologically stable island presumably would also reduce the chance of speciation occurring.

A relatively recent time of divergence for *Clermontia* also may be supported by data on host plant specificity among the endemic picture-winged species of fruit flies (*Drosophila*). Members of this group use rotting tissues (stems, roots, leaves, flowers, fruits) of various plants as ovipositing sites and larval substrata; species of Lobelioideae are among the most commonly used (Heed, 1971; Carson and Kaneshiro, 1976). According to Spieth (1982), use of *Cyanea* is a plesiomorphic trait, and use of *Clermontia* derived. However, the only species of *Clermontia* exploited by picture-winged flies are those on the younger islands; those on the older islands such as Kaua'i and O'ahu are not. This fact might be explained by a very recent arrival of the plants on those islands, long after host plant relationships between picture-winged *Drosophila* and the indigenous flora had developed. In other words, it may be that none of the

picture-winged species on O'ahu or Kaua'i has had time to adapt to the newly arrived species of *Clermontia* there.

Any number of alternative hypotheses regarding time and place of origin might be put forth: that *Clermontia fauriei* actually represents the basal lineage, and thus the genus originated as much as 5.1 million years ago (Ma) on Kaua'i; that *C. clermontioides* is indeed the basal lineage but once occurred on older islands, thus pushing back its time of divergence; or that the genus diverged on much older islands no longer capable of supporting lobelioids, but that all the basal taxa are extinct, leaving only the products of a more recent secondary radiation. Although worthy of further consideration as new data become available, none of these hypotheses find support in the current analysis.

If indeed the genus originated on Hawai'i, the first diversification would have involved the three species of series *Clermontioideae*. These species are largely allopatric or at least parapatric, as are the two subspecies that comprise *Clermontia clermontioides* (see Table 15.1).

Although the island of Hawai'i may be the point of origin for the genus, its center of diversification clearly was the Maui Nui complex. The area cladogram suggests that very early in its history, the genus dispersed from Hawai'i to this older island. Once established there, it apparently diverged into the two main clades that compose the remainder of the genus: the clade comprising series *Sarcanthae* and series *Unilabiatae*, and that comprising section *Clermontia*.

The *Sarcanthae*-*Unilabiatae* clade diverged into two subclades, representing the two taxonomic series. The *Sarcanthae*, which consists of two species (one divided into three subspecies), diversified entirely within the Maui Nui complex. The most plesiomorphic member of this clade is *Clermontia arborescens* subsp. *waikoluensis* of Moloka'i and Lana'i. The remaining taxa of *Sarcanthae* are endemic to Maui, but nonetheless are largely allopatric or at least parapatric. For example, both *C. arborescens* subsp. *arborescens* and *C. arborescens* subsp. *waihia* occur on West Maui, but the range of the former lies south of the latter; similarly, both *C. tuberculata* and *C. arborescens* subsp. *waihia* occur on East Maui, but the former grows at higher elevations than the latter (Lammers, 1991).

In contrast to their sister group, the *Unilabiatae* species have dispersed throughout the remainder of the archipelago. The most plesiomorphic member of this clade is *Clermontia peleana* subsp. *singuliflora*. This subspecies apparently originated on East Maui and then dispersed to the windward slopes of Mauna Kea on Hawai'i. There, it is

assumed to have given rise to subspecies *peleana*, which spread southward to windward Mauna Loa. From the Maui Nui complex, this subclade also dispersed to O'ahu, the next older island. This dispersal event was accompanied by speciation, resulting in *C. fauriei*. From O'ahu, this species must have colonized the yet older island of Kaua'i, the only member of the genus to have done so. Once again, all members of the clade are allopatric or at the very least parapatric.

The clade comprising section *Clermontia* diverged on the Maui Nui complex into two subclades, the *Parviflorae* clade and the clade comprising the autonymic series, as well as the metaphyletic *Kakeanae*. All three of these groups have diversified on Maui Nui and also dispersed onto O'ahu and Hawai'i.

Within section *Clermontia* as a whole, as well as among the *Kakeanae*, *C. kakeana* is the species with the fewest apomorphies. It is presumed to have originated on windward Maui and Moloka'i and subsequently dispersed to O'ahu. Despite this relatively broad distribution, the populations are sufficiently similar that no subspecies have been recognized (i.e., inter-island dispersal was not accompanied by any significant divergence). The distribution of *C. lindseyana* may be accounted for by assuming an origin on leeward East Maui and subsequent dispersal to the younger island of Hawai'i.

In addition to these two species, the *Kakeanae* include two small poorly supported clades. The first comprises *Clermontia pallida*, which is endemic to Moloka'i, and *C. persicifolia*, which is the result of dispersal to O'ahu. The second clade comprises three "black-flowered" species endemic to Hawai'i: *C. drepanomorpha*, *C. kohalae*, and *C. montis-loa*. Thus, two more inter-island dispersal events must be inferred, both accompanied by speciation.

The clade comprising the autonymic series underwent most of its diversification in the Maui Nui complex. This series includes nine taxa (five species plus four heteronymic subspecies), seven of which are restricted to various parts of Maui Nui (see Table 15.1). Most are allopatric, although some are partially sympatric (e.g., *Clermontia oblongifolia* subsp. *mauiensis* and *C. grandiflora* subsp. *munroi* on West Maui). The two occurring elsewhere are *C. hawaiiensis*, endemic to Hawai'i, and *C. oblongifolia* subsp. *oblongifolia*, endemic to O'ahu. Thus, two more inter-island dispersal events are inferred, one accompanied by speciation and the other by a lesser degree of morphological differentiation.

The *Parviflorae* clade is likewise inferred to have originated in the Maui Nui complex, where *Clermontia micrantha* (West Maui and Lana'i)

TABLE 15.3. Summary of Inter-island Dispersal Patterns in *Clermontia*, Assuming an Origin on the Island of Hawai'i

| Pattern | With speciation | Without speciation |
|------------------------------|-----------------|--------------------|
| From younger to older island | | |
| Hawai'i to Maui Nui | 1 | 0 |
| Maui Nui to O'ahu | 2 | 3 |
| O'ahu to Kaua'i | 0 | 1 |
| From older to younger island | | |
| Maui Nui to Hawai'i | 3 | 2 |
| Total | 6 | 6 |

and the extinct *C. multiflora* (West Maui) occur; the latter also dispersed to O'ahu. A single dispersal event to Hawai'i is inferred for the largely allopatric *C. calophylla* and *C. parviflora*.

These biogeographic hypotheses are integrated and summarized in Table 15.3 and Figure 15.6. First, in *Clermontia*, speciation has occurred most often within an island and is not strongly correlated with inter-island dispersal. Of the 22 speciation events, only 6 were associated with inter-island dispersal. The remaining 16 occurred within an island, most commonly Maui Nui.

Second, the species of *Clermontia* inhabiting a given island do not constitute any sort of clade or natural group but rather form a heterogeneous assemblage drawn from several distinct lineages. For example, none of the species on O'ahu belong to the same clade. Thus, they are not the products of radiation from a single colonization but rather the products of five separate colonizations. Further, none of these lineages underwent further speciation; the five lineages that colonized the island from Maui Nui are represented by just five species, only two of which do not occur on Maui Nui. This contrasts with the situation on Hawai'i, where two of the five colonizing lineages from the Maui Nui complex underwent further speciation; altogether, these five colonists yielded eight species, six of which do not occur on Maui Nui. If one assumes that a greater period of occupation correlates with more opportunities for speciation, then this is additional evidence that *Clermontia* has been present on the younger islands for a longer period of time and that it is a relatively recent arrival on the older islands.

Third, inter-island dispersal in this genus is about as likely to have resulted in speciation as not. A minimum of 12 inter-island dispersal

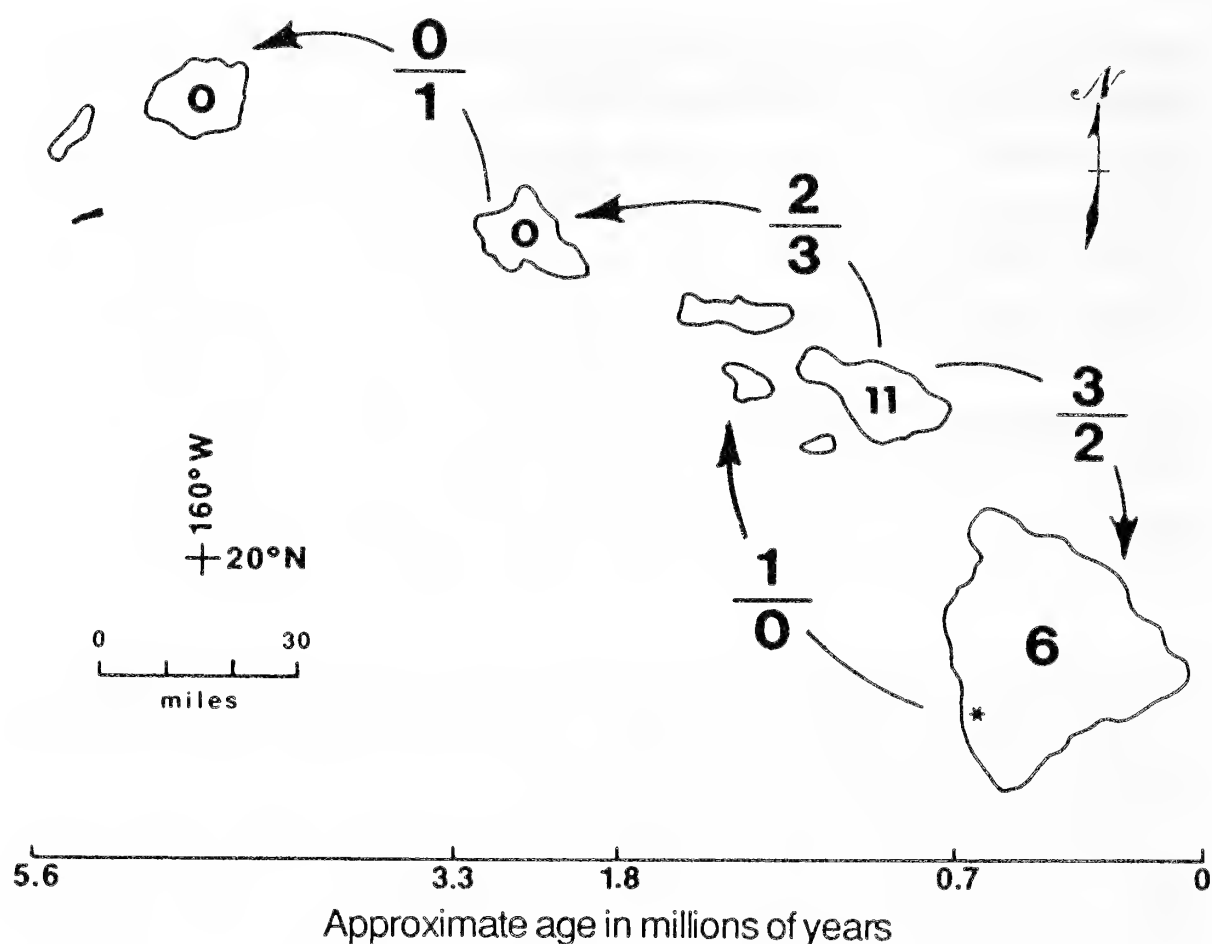


FIGURE 15.6. Summary of the diversification and spread of *Clermontia* in the Hawaiian archipelago. Numbers on islands indicate the number of intra-island speciation events. Fractions on arrows refer to inter-island dispersal events; the numerator indicates the number of such events that were accompanied by speciation, and the denominator indicates the number that were not accompanied by speciation.

events are required to explain the historically known distribution of *Clermontia* (Table 15.3). Six of these were associated with speciation; the other six were not but merely served to expand the distribution of the species.

Fourth, it appears that it may have been easier for *Clermontia* to disperse onto an older island than onto a younger one. Seven of the 12 dispersals were from younger islands to older islands; just 5 were from older to younger (Maui Nui to Hawai'i). As noted previously, this is contrary to the pattern seen in most Hawaiian angiosperms. Younger volcanic islands are presumed to be easier to colonize because of their many unfilled niches and geologically dynamic nature, whereas older, biotically stable islands present fewer opportunities for colonization. The ability of *Clermontia* to "swim upstream" may be related to its observed ecological role as a pioneer on edges, openings, and windfalls in the forest

rather than as a member of a stable climax community. The genus's pronounced trend toward epiphytism may also play a role in its ability to invade older islands.

As noted above, the frugivorous 'O'u is a particularly likely candidate for a major role in the dispersal of *Clermontia*. This bird formerly occurred in montane forests on the six largest islands. The 'O'u is much less sedentary than other drepanids, often wandering over great distances, typically in large flocks (Perkins, 1903; Amadon, 1950). Geographic races are not discernible, which suggests gene flow sufficient to forestall divergence (i.e., that inter-island flights occur rather frequently, at least on an evolutionary time scale) (Amadon, 1950; Grant, 1981). These characteristics may have made it an important vector in the inter-island spread and diversification of *Clermontia*.

Elucidation of the processes by which new species arise is best achieved through the synthesis of diverse data from biosystematic, genetic, and molecular studies (Crawford et al., 1987). However, as such data are not likely to be available for *Clermontia* in the foreseeable future, it seems useful to make some statement about process on the basis of the inferred evolutionary and geographic patterns.

In most instances, speciation in *Clermontia* appears to have occurred allopatrically. As noted above, the members of a given clade typically occur on different islands or on different parts of one island. Of the various modes of allopatric speciation described by Grant (1981), two may have been operative in *Clermontia*: quantum speciation and geographic speciation.

Quantum speciation involves the production of novel species from a random subset of the progenitor's gene pool, through the intermediate stage of an allopatric (or possibly parapatric) peripheral population. Clearly, an archipelago is the ideal setting for the establishment of such populations via stochastic founder events (Crawford et al., 1987). A combination of drift and selection drives divergence, as do the effects of inbreeding. Inbreeding in peripheral isolates may result from the small initial population size characteristic of founder events or from self-fertilization. Geographic speciation is very similar to quantum speciation but is more gradual and conservative, involving divergence of species from local races through the intermediate stage of geographic races. However, the two are very difficult to discern without detailed genetic data.

One might suggest that quantum speciation was operative in those cases involving inter-island dispersal (e.g., *Clermontia fauriei* and *C. persicifolia*) and geographic speciation in those cases involving divergence

within an island (e.g., *C. kohalae* and *C. montis-loa*, or the three species of series *Clermontioideae*). Possible examples of intermediate levels of divergence might include the three subspecies of *C. oblongifolia*, each on a separate island, and the two parapatric subspecies of *C. arborescens* on West Maui.

Also, a few examples may represent sympatric speciation from ecological races. Two of the species of the black-flowered *Kakeanae* clade are sympatric in the Kohala Mountains but occur in different habitats: *Clermontia drepanomorpha* in open bogs and *C. kohalae* in forested valleys. The two sympatric subspecies of *C. grandiflora* on West Maui may represent an earlier stage of such divergence: subspecies *grandiflora* occurs in open bogs and subspecies *munroi* in the surrounding forest.

Despite the occurrence of sporadic hybridization on a homoploid level (Lammers, 1991), there is no evidence of hybrid origin for any species. The uniformity of chromosome numbers in the genus and its relatives (Lammers, 1988, 1993) precludes the possibility of allopolyploid speciation.

One final aspect of speciation remains to be addressed. In an isolated and physiographically diverse environment such as the Hawaiian Islands, speciation often is a result of the phenomenon of adaptive radiation. This is best defined as the evolution from a single ancestral stock of a large number of species adapted in striking or unusual ways to a diverse array of niches (Carlquist, 1974; Crawford et al., 1987). This definition thus embraces phylogenetic, ecological, and morphological criteria. Only groups that satisfy all three criteria may properly be regarded as examples of adaptive radiation.

Are the species of *Clermontia* the product of adaptive radiation? The genus certainly fulfills the phylogenetic criterion: A single ancestor has given rise to 22 known species, possibly in a very short span of time. However, the ecological amplitude of the genus is hardly remarkable when compared with other species-rich Hawaiian lineages. None of the species occur in the coastal, subalpine, or alpine zones, in dry communities of the lowland or montane zones, or in grasslands, sedgelands, or herblands at any elevation (Gagné and Cuddihy, 1990). Most populations lie within an elevational band just 1,000 m wide; the entire range occupied by the genus is little more than 2,000 m. Further, *Clermontia* shows very little variation in habit and vegetative morphology. There are no herbs, subshrubs, large trees, cushion plants, lianas, unbranched palmlike trees, or monocarpic rosette plants. This uniformity of habit is reflected in the interspecific homogeneity of wood anatomy (Carlquist, 1969a). The

leaves are remarkably similar from one species to the next, with only minor differences in size, outline, thickness, and pubescence.

It might be argued that the remarkable variation in floral morphology within *Clermontia* would constitute adaptation in striking or unusual ways to a diverse array of niches. Although this variation is indeed striking, it is not correlated with utilization of diverse niches. All evidence points to a single class of pollinators, passerine birds, for not only *Clermontia* but for nearly all the Hawaiian lobelioids (Lammers and Freeman, 1986). If different species of *Clermontia* were pollinated by not only passerine birds but also by short-tongued bees, long-tongued bees, butterflies, hawk moths, and settling moths, the genus could indeed be considered to have occupied a diverse array of niches. As it is, *Clermontia* has occupied but a single pollinator niche. For this reason, the species of *Clermontia* really cannot be considered a good example of adaptive radiation in an insular environment.

SUMMARY

Comparison of the inferred phylogeny of *Clermontia* to the documented geographic distribution of the genus suggests the following: *Clermontia* diverged on the youngest island, Hawai'i, sometime about 500 to 700 ka; from there, the genus spread throughout the six largest islands of the archipelago, giving rise to 22 known species; only 27% of the 22 inferred speciation events were associated with inter-island dispersal, the remainder occurring within an island; only half of the 12 inferred inter-island dispersal events resulted in speciation, the remainder serving only to expand the range of a species; only 42% of the 12 inferred inter-island dispersal events proceeded from an older to a younger island, which is by far the most common pattern among Hawaiian angiosperms; the species inhabiting a given island are a heterogeneous assemblage drawn from several distinct lineages rather than a monophyletic group; allopatric modes of speciation (quantum speciation, geographic speciation) appear to have been most common in the genus, although a few cases may represent sympatric speciation from ecological races; although the genus includes a large number of species descended from a common ancestor and shows striking diversity in floral morphology, the genus has not occupied a diversity of niches and thus should not be cited as an example of adaptive radiation.

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APPENDIX 15.1. Character List for *Clermontia*

Characters 2, 7, 8, 17, 19, 23, and 30 were treated as unordered.

Stem and Leaves

1. Stem: 0 = sparingly branched; 1 = repeatedly branched.
2. Leaf margin: 0 = denticulate; 1 = crenulate; 2 = serrulate.
3. Petiole color: 0 = opaque green; 1 = translucent yellowish-white.
4. Petiole shape: 0 = terete; 1 = winged.
5. Petiole length: 0 = less than $\frac{1}{2}$ as long as lamina; 1 = $\frac{1}{2}$ as long as lamina or more.

Inflorescence

6. Number of flowers per peduncle: 0 = 6–12; 1 = commonly 2, though sometimes as many as 5; 2 = commonly 1 via abortion.
7. Peduncle length: 0 = $\frac{1}{2}$ –3 times as long as pedicel; 1 = less than $\frac{1}{2}$ as long as pedicel; 2 = 3–5 times as long as pedicel.
8. Peduncle posture: 0 = spreading; 1 = declinate; 2 = pendent.
9. Pedicel rigidity: 0 = stiff; 1 = flexuous.

Hypanthium

10. Shape: 0 = widest at apex; 1 = widest below apex.
11. Surface: 0 = smooth or with 10 shallow furrows; 1 = with 10 prominent ridges.

Calyx lobes

12. Persistence: 0 = persistent on the fruit; 1 = deciduous with corolla.

- 13. Fusion: 0 = distinct; 1 = connate.
- 14. Color: 0 = matches hypanthium; 1 = matches corolla.
- 15. Texture: 0 = sepaloid; 1 = petaloid.
- 16. Shape: 0 = triangular; 1 = linear.
- 17. Length: 0 = less than $\frac{1}{2}$ as long as corolla; 1 = $\frac{2}{3}$ as long to as long as corolla; 2 = as long as corolla.

Corolla

- 18. Tube integrity: 0 = dorsally cleft to middle; 1 = dorsally cleft to base.
- 19. Tube curvature: 0 = gently curved; 1 = erect or suberect; 2 = arcuate.
- 20. Lobe length: 0 = equaling or exceeding tube; 1 = $\frac{1}{5}$ – $\frac{1}{2}$ as long as tube.
- 21. Lobe length: 0 = all 5 of equal length; 1 = dorsal 2 longer than ventral 3.
- 22. Lobe posture: 0 = spreading or suberect; 1 = strongly recurved.
- 23. Lobe position: 0 = bilabiate; 1 = unilabiate; 2 = rotate.
- 24. Texture: 0 = firm; 1 = fleshy.
- 25. Overall length: 0 = 3–9 cm; 1 = 1.5–3 cm.
- 26. Surface: 0 = glabrous or pubescent; 1 = muricate.
- 27. Internal color: 0 = green, white, light purple, magenta, or rose; 1 = dark purple.

Staminal column

- 28. Exsertion: 0 = included or slightly exserted; 1 = strongly exserted.
- 29. Curvature: 0 = matches corolla curvature; 1 = diverges sharply from corolla.
- 30. Anther tube length: 0 = 3–4 times longer than wide; 1 = 2–3 times longer than wide; 2 = 4–5 times longer than wide.

Fruit

- 31. Berry size: 0 = 0.5–2 cm long; 1 = 2–4 cm long.
- 32. Pericarp: 0 = thin; 1 = thick.

APPENDIX 15.2. Data Matrix of Character States Used in the Cladistic Analysis of *Clermontia*

The characters and character states are defined in Appendix 15.1, and species abbreviations are spelled out in Table 15.1. Missing data are indicated by question marks.

| Character | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | |
| out | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| ARB | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | |
| CAL | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| CLE | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| DRE | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| FAU | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| GRA | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| HAW | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| KAK | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| KOH | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| LIN | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| MIC | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| MON | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| MUL | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| OBL ₀ | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| OBL _M | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| PAL | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| PAR | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| PEL _p | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 1 |
| PEL _s | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 |
| PER | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| PYR | 1 | 2 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| SAM | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| TUB | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| WAI | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |

16

Phylogenetic Analysis of Hawaiian and Other Pacific Species of *Scaevola* (Goodeniaceae)

ROBERT PATTERSON

The Pacific biota is often cited for its high level of species-level endemism. Major factors promoting high endemism involve colonization from one or more source areas, followed by radiation, sometimes adaptive radiation (Carlquist, 1980). An example of this pattern is found in the genus *Scaevola* (Goodeniaceae) (Figure 16.1), represented on Pacific oceanic islands by 22 species, endemic to various archipelagoes (excluding Philippine species) (Table 16.1), and one other widespread coastal species. *Scaevola* is 1 of 15 genera of Goodeniaceae, consisting of about 100 species, most of which occur in western Australia. In addition to *Goodenia*, *Scaevola* is the only genus in the family with a large number of species and the only one with a substantial number of species that occur outside of Australia. In a recent treatment of the genus, Carolin (1990) recognized five sections, of which section *Scaevola*, consisting mainly of the Pacific species, is predominantly extra-Australian. Section *Scaevola* is most readily distinguished from the other sections by its drupaceous fruits instead of the dry fruits characteristic of most Australian species. These fleshy fruits appear to be readily disseminated by birds, and therefore the Pacific species have been regarded as derived from ancestors via long-distance dispersal (Carlquist, 1974). The single widespread Pacific species, *S. sericea*, has specialized fruit and is dispersed by oceanic drift (Carlquist, 1974). Most endemic Pacific *Scaevola* are shrubs or small trees of upland habitats, although lowland species occur in New Caledonia and the Hawaiian Islands.

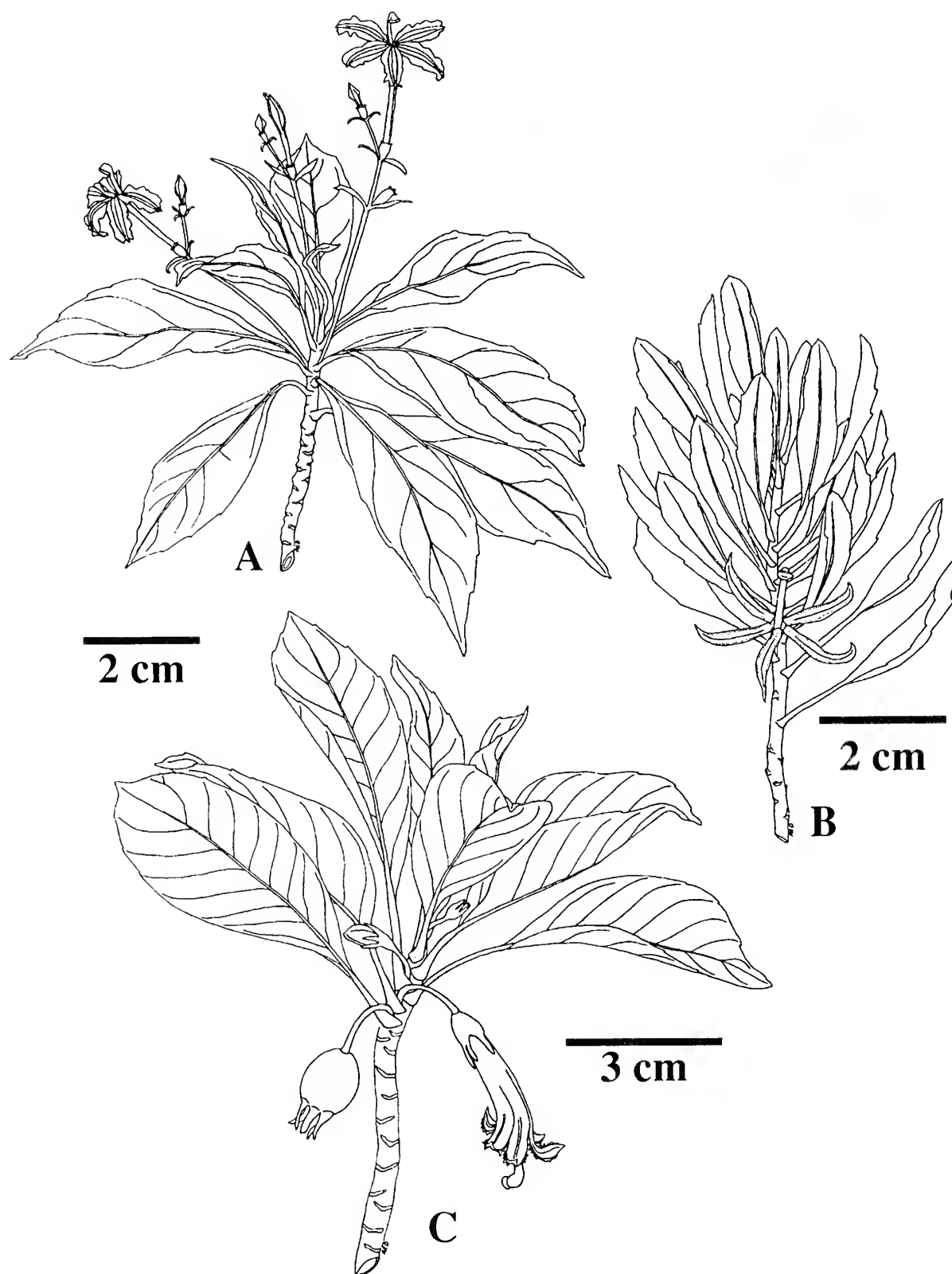


FIGURE 16.1. Hawaiian *Scaevola* species. (A) *S. gaudichaudiana*; (B) *S. gaudichaudii*; (C) *S. glabra*.

There are eight endemic species in the Hawaiian Islands (Table 16.1). *Scaevola glabra* (Figure 16.1C) is readily distinguishable from the other Hawaiian endemics by several autapomorphies. Its thick-textured, curved, bright yellow corollas (bird-pollinated) are strikingly different from those of any other Hawaiian species. The flowers of other Hawaiian

TABLE 16.1. Pacific Species of *Scaevola* Section *Scaevola* (except *S. sericea*)

| Region and species ^a | Islands | Habitat ^b |
|--|--|--------------------------------------|
| Hawaiian Islands | | |
| * <i>S. chamissoniana</i> Gaud. | Moloka'i; Lana'i; Maui; Hawai'i | Wet forests |
| * <i>S. coriacea</i> Nutt. | All main islands | Coastal strand |
| * <i>S. gaudichaudiana</i> Cham. | Kaua'i; O'ahu | Wet forests |
| * <i>S. gaudichaudii</i> Hook. & Arnott | All main islands | Dry ridges and scrublands |
| * <i>S. glabra</i> Hook. & Arnott | Kaua'i; O'ahu | Wet forests |
| * <i>S. kilaueae</i> Degener | Hawai'i | Open forests and scrublands |
| * <i>S. mollis</i> Hook. & Arnott | Kaua'i; O'ahu; Moloka'i | Wet forests |
| * <i>S. procera</i> Hillebr. | Kaua'i; Moloka'i | Wet forests |
| Marquesas Islands | | |
| * <i>S. marquesensis</i> F. Brown | Hiva Oa | Wet forests |
| * <i>S. subcapitata</i> F. Brown | Fatu Hiva; Hiva Oa; Nuku Hiva; Ua Huka | Wet forests |
| Society Islands | | |
| * <i>S. tahitiensis</i> Carlquist | Tahiti | Wet forests |
| Samoa | | |
| * <i>S. nubigena</i> Lauterb. | Savai'i | Wet forests |
| Fiji | | |
| * <i>S. floribunda</i> A. Gray | | Wet forests |
| Irian Jaya | | |
| <i>S. pauciflora</i> Leenh. | | Unknown |
| New Caledonia | | |
| <i>S. balansae</i> Guillaumin | | Maquis and forests |
| <i>S. beckii</i> Zahlbr. | | Maquis and forests |
| * <i>S. coccinea</i> Däniker | | Serpentine regions |
| <i>S. cylindrica</i> Schlechter & K. Krause | | Maquis and wet forests |
| <i>S. erosa</i> Guillaumin ex I. H. Müller | | Maquis and forests |
| * <i>S. montana</i> Gaud. | | Serpentine and calcareous regions |
| <i>S. racemigera</i> Däniker | | Montane |

^aAsterisks denote species included in the phylogenetic analysis.
^bHabitat data for Hawaiian Islands and New Caledonia species taken from Patterson (1990) and Müller (1990), respectively.

species are usually fragrant and appear to be primarily insect-pollinated. *Scaevola glabra* also has fruits that are four to five times the fruit size of the other endemics, suggesting to Carlquist (1969b, 1974) that they exemplify a loss of dispersibility. *Scaevola glabra* is furthermore a tetraploid ($2n = 32$), whereas all other Hawaiian species are diploids ($2n = 16$). These various differences have been used by some authors to recognize *S. glabra* as a separate genus, *Camphusia*.

Carlquist (1969b, 1974, 1980) discussed the pattern of how closely related species have radiated into diverse habitats. Patterson (1984a), however, addressed the lack of diversification among Hawaiian species based on flavonoid characters, suggesting a low level of genetic divergence since their radiation into different habitats on different islands. Gillett's (1966) examination of hybridization among certain Hawaiian *Scaevola* species also emphasized their evolutionary similarity. Despite the close morphological similarity of some of the Hawaiian species and the small differences in flavonoid characters, the nine species indigenous to the Hawaiian Islands are reasonably well distinguished from each other each by a few features (Patterson, 1990).

The eight endemic New Caledonian species are also morphologically similar to each other and, to a lesser degree than in the Hawaiian Islands, appear to occupy an array of habitats (Müller, 1990), but extensive systematic study of these plants has not been undertaken. The endemic species of *Scaevola* on Tahiti (one), the Marquesas (two), Samoa (one), and Fiji (one) are similar to each other morphologically, differing with few exceptions by subtle features, primarily inflorescence characters. The relationships among these species have not been investigated.

Carolin (1990) provided a cladistic analysis of many species of *Scaevola* that provides insight to relationships within the genus, including within and among section *Scaevola*. His focus, however, was on overall relationships within the entire genus, and thus he did not concentrate on relationships among the Pacific taxa. For example, in his data set he regarded *S. gaudichaudiana*, *S. procera*, and *S. chamissoniana* as a combined taxon group (although *S. procera* is also listed as a terminal taxon) and *S. floribunda* (Fiji), *S. tahitiensis* (Tahiti), and *S. montana* (New Caledonia) as another combined group. He also excluded five Pacific species from his study, including *S. nubigena* (Western Samoa), *S. balansae*, *S. cylindrica*, *S. erosa*, and *S. macropyrena* (New Caledonia). Consequently, his study provided noteworthy but limited information with regard to relationships among the Pacific species.

This chapter addresses phylogenetic relationships of the Pacific species of *Scaevola* based on available morphological data. The goals of the study are to explore biogeographic patterns within section *Scaevola* and specifically to examine the hypothesis that Hawaiian *Scaevola* species represent at least three separate introductions as proposed by Gillett (1966), Carlquist (1974), and Patterson (1984b).

MATERIALS AND METHODS

The terminal taxa selected for study include the nine species indigenous to the Hawaiian Islands plus representative species endemic to other Pacific islands (Table 16.1). Only two of eight New Caledonian endemics were included, as was only one Marquesan endemic. Species from the Malesian area were not included nor was the widespread *Scaevola plumieri* (L.) Vahl.

Earlier authors working on Hawaiian *Scaevola*, in particular St. John (1973), recognized many infraspecific taxa and occasionally additional species. Although further study is needed to determine the level of intricacy of infraspecific variation in Hawaiian *Scaevola* species, this chapter concentrates on species-level relationships.

Because the relationship among Hawaiian species is the principal focus of this study, several outgroup species were included from within the Pacific members of section *Scaevola* as well as several members of other sections of the genus. *Scaevola montana* was used as the outgroup in the final analysis for several reasons: It provided the shortest and clearest trees; it has fewer specialized features that might compromise its effective use as an outgroup; and it is geographically closer to Australia, the location of most species of *Scaevola*. The other endemic Pacific species (*S. subcapitata*, *S. tahitiensis*, *S. nubigena*, and *S. floribunda*) were sampled as outgroups based on the assumption that any of the islands where they occur might be a likely source for the first Hawaiian colonist; however, they did not provide any more reasonable analysis than trees constructed using *S. montana* as the outgroup. Members of other sections of *Scaevola* were also tried as possible outgroups, but their use offered no advantage over *S. montana*. Although use of *S. montana*, a member of section *Scaevola*, cannot help resolve phylogenetic relationships of all members of that section, it can serve to polarize characters used in analyzing the non-New Caledonian members of the Pacific species. Further study of relationships that include New Caledonian species will need to rely on other choices for an outgroup.

After eliminating autapomorphies, uninformative characters, and characters for which data were not available for all species (except in the outgroup), 15 morphological characters were selected for use in the phylogenetic analysis (Appendixes 16.1 and 16.2). The Pacific *Scaevola* species are morphologically very similar in their vegetative and floral morphology, and many of the features by which they have been distinguished are not discrete characters. Although Carolin (1990) used 26 morphological characters in his cladistic analysis of the genus, few of these were useful in analyzing the Pacific species. An attempt was made to restrict the use of characters to those in which discrete differences occur among character states. For example, degree of pubescence on various organs is variable in *Scaevola* despite its occasional use as a diagnostic feature. It was used in the present data set only in clear cases of organs being either densely pubescent or glabrous. Likewise, measurement data that overlap between species pairs (e.g., petiole length) were not used in this study. Many of the features by which certain species are commonly distinguished, such as habit, leaf shape, and corolla color, were not used in this study because they were too variable to allow explicit coding.

Phylogenetic analyses were conducted using PAUP version 3.1.1 (Swofford, 1993). Multistate characters were treated as unordered given that no particular information is available that addresses character state evolution in this group. The branch-and-bound option was used to search for the most-parsimonious trees using the furthest addition sequence option. MacClade version 3.0 (Maddison and Maddison, 1992) was also used to examine character evolution and explore alternative trees. An area cladogram was constructed to explore patterns of distribution based on the phylogenetic analysis.

RESULTS

The preliminary analysis resulted in one most-parsimonious tree, 35 steps in length, with a consistency index (CI) of 0.457 (Figure 16.2). The low CI value reflects a very high incidence of homoplasy—only 1 of the 15 characters is uniquely derived—with some appearing as parallelisms as many as four times on a tree. Removal of various characters that showed a high degree of homoplasy still resulted in relatively low CI values. Although it is clear that such homoplasy places severe constraints on the value of the information provided by the trees generated, it does not

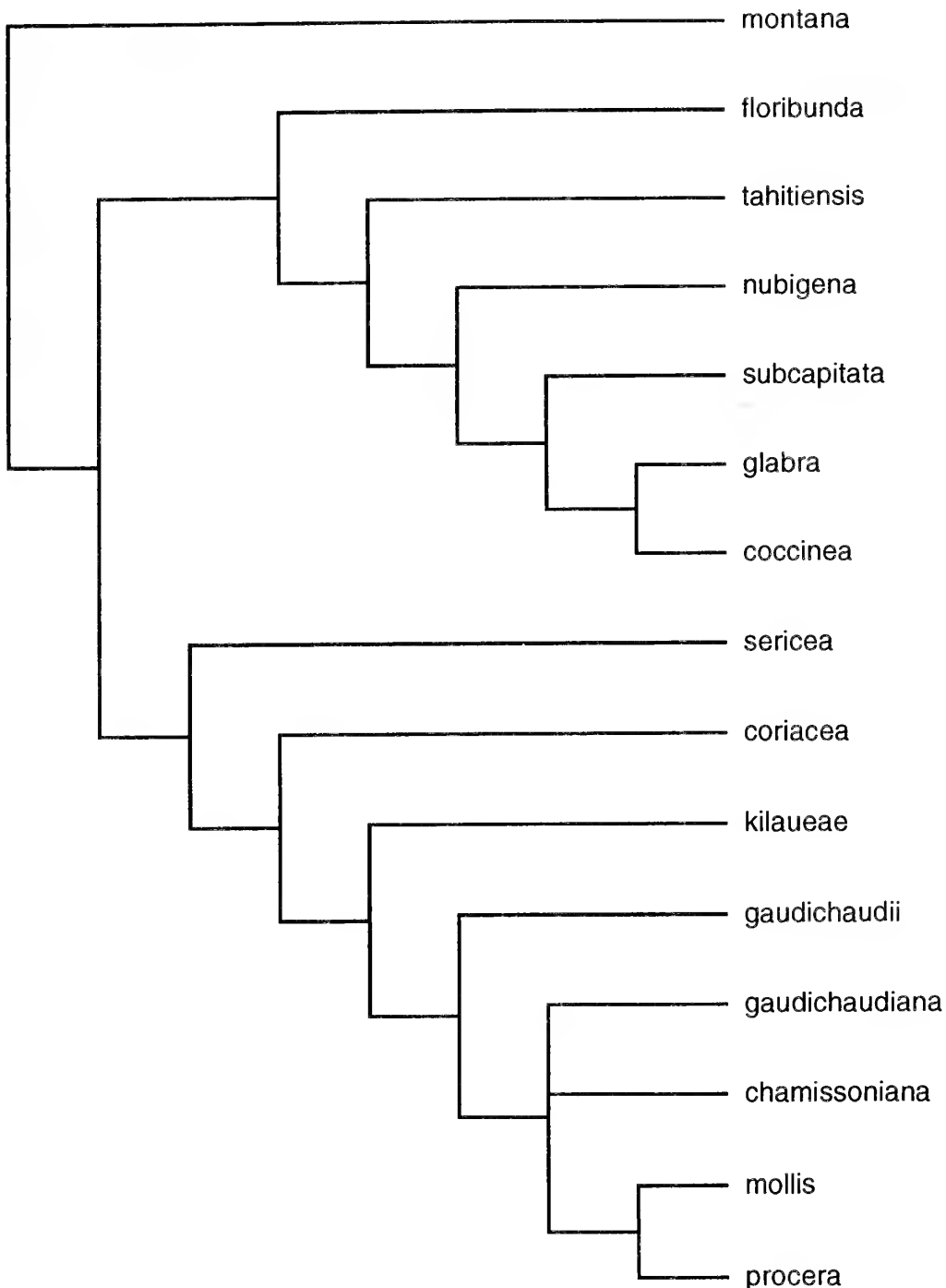


FIGURE 16.2. Single most-parsimonious cladogram of Pacific *Scaevola* based on 15 morphological characters. Total length, 35 steps; CI, 0.457. The outgroup was *S. montana*.

prevent the trees from being used to suggest particular patterns that may be pursued as additional data become available for analysis.

The analysis resolves the Hawaiian diploid endemics as a monophyletic group, with *Scaevola sericea* appearing as the sister group to the Hawaiian diploids. Within the diploid clade, the mesic-habitat species arise as a monophyletic group, and the dry-habitat species are basal to it. The remaining Pacific species arise sequentially as follows: *S. floribunda*, *S. tahitiensis*, *S. nubigena*, *S. subcapitata*, and the species-pair *S. coccinea*–

S. glabra. This result suggests at least two separate introductions of *Scaevola* to the Hawaiian Islands and is consistent with the currently held view of three independent introductions.

DISCUSSION

The low CI (0.457) showing a high level of homoplasy places considerable constraint on the ability of this analysis to explain phylogenetic relationships. Most of the discrete characters used appear to have evolved in more than one lineage. Other morphological characters that have been used previously to distinguish Pacific species either are not discrete or show enough variability to preclude their use in a cladistic analysis. Consequently, caution must be used in interpreting the results obtained here. Nevertheless, the data presented are useful in suggesting particular patterns that may be tested as additional characters become available for analysis.

Relationships among Hawaiian *Scaevola* Species

Carlquist (1969b) used morphological and ploidal differences to suggest that *Scaevola glabra* was not a member of the Hawaiian diploid endemic lineage and that the closest relative of *S. glabra* may be from New Caledonia. The analysis provided here is in accord with the notion that ancestors of *S. glabra* may have reached the Hawaiian Islands during a separate colonization than that bringing the ancestor of the diploid endemics. Examination of Müller's (1990) floristic treatment of New Caledonian *Scaevola* does not suggest any likely candidates for ancestry based on a cursory examination of her descriptions or illustrations. *Scaevola coccinea* appears to be closest and is the sister species in the single tree obtained in this analysis. Further study of New Caledonian species is warranted to corroborate *S. coccinea* as the closest relative of *S. glabra*.

The remaining seven diploid Hawaiian endemics represent a well-defined monophyletic group. Carlquist (1974) suggested that Hawaiian plant species generally derive from ancestors in drier localities; thus, Hawaiian species radiating into wetter habitats may reflect more recently derived taxa. This pattern is in accord with the trees produced in this study. *Scaevola coriacea*, a historically widespread (although presently rare and restricted to Maui and Moloka'i) strand species, appears as the sister group to the rest of the diploid endemics. It is restricted and highly

adapted to strand habitats, from where it is easy to visualize an early radiation of strand versus inland taxa, given the assumption that the ancestor to the entire lineage made landfall at or near the shoreline. Radiation from a putative common ancestor into such a habitat would have been a large departure from species radiating into inland habitats. Structural and physiological adaptations to strand areas would be different from those associated with radiation into upland regions. Carlquist (1969b) suggested that *S. coriacea* might be a derivative of *S. gaudichaudiana*, but this suggestion is not supported by phylogenetic analysis.

The narrowly restricted *Scaevola kilaueae* and the widespread *S. gaudichaudii* are respectively sequential on the tree above *S. coriacea*. Although both species occur in relatively dry habitats, their distributions suggest different patterns of evolution. The latter is the most widespread Hawaiian species in terms of its distribution on six of the main Hawaiian Islands, whereas the former is a narrowly restricted species. The narrow distribution of *S. kilaueae* could be explained by a recent derivation. *Scaevola kilaueae* does bear resemblance to *S. chamissoniana*, the widely distributed forest species on Hawai'i, but there is no phylogenetic evidence suggesting that the former is derived from the latter. The widespread distribution of *S. gaudichaudii* suggests that this species had an earlier origin than *S. kilaueae* and was capable of considerable dispersal. This line of reasoning is in conflict with the phylogeny. Further morphological differentiation and speciation into xeric habitats within this clade has not occurred, as has apparently been the case in the mesic-habitat clade.

Scaevola gaudichaudii is readily distinguished from any other Hawaiian species by lack of wings on the corolla lobes (see Figure 16.1B), a feature also shared with Marquesan, Tahitian, and Samoan species. Without the cladistic approach to character analysis in Hawaiian *Scaevola* species, it might be tempting to view the particular features of *S. gaudichaudii* as indicative of a more distant relationship with the other species. It is, however, clearly nested within the Hawaiian clade.

The unique corolla morphology of *Scaevola gaudichaudii*, with brownish yellow wingless lobes, stands apart from that of any of the other species, implicating a different pollination system from that of the other diploid Hawaiian endemics. The reproductive biology of Hawaiian *Scaevola* species has only been examined cursorily (Carlquist, 1974) and may provide interesting clues to patterns of evolution in the Hawaiian members of the genus.

The four wet-forest species (*Scaevola mollis*, *S. procera*, *S. chamissoniana*, and *S. gaudichaudiana*) constitute a monophyletic group. *Scaevola gaudichaudii* is the sister group to the mesic-taxon lineage (*S. chamissoniana*, *S. gaudichaudiana*, *S. mollis*, and *S. procera*). *Scaevola chamissoniana* and *S. gaudichaudiana* (see Figure 16.1A) differ by few features, most of which are based on continuous size measurements. The only character that could be coded discretely is stamen length relative to corolla length, and although there is disjunction between character states, even this feature must be regarded with caution. Without the stamen length character, these species are impossible to distinguish in this analysis given the available data. Combining them does not alter the parsimony trees substantially. They are mutually exclusive on a given island, and it is likely that their distinction, however slight, is reinforced by their restriction to certain islands.

Whether these species represent distinct taxa or whether they actually represent a single species needs to be ascertained by other modes of analysis. Assuming that speciation has resulted in the older-island *S. gaudichaudiana* and the younger-island *S. chamissoniana*, it is tempting to invoke a scenario related to age of islands. For example, following the evolutionary event that finally separated the clade ancestral to *S. gaudichaudiana* and *S. chamissoniana* from the one ancestral to *S. mollis* and *S. procera*, and assuming that this ancestral clade was present on all islands, differences between older and younger islands could have been responsible for selection and subsequent speciation into the two existing species. However, the respective habitats for each species on older versus younger islands is similar, making it difficult to suggest that habitat differences affected differentiation of these taxa. An alternative explanation for the differentiation of these species is that differentiation (e.g., of *S. chamissoniana*) followed dispersal of propagules of its ancestor from older islands, yet the phylogenetic evidence does not suggest such a model. A third possibility is that *S. chamissoniana* and *S. gaudichaudiana* do not really represent distinct species and that this taxon is present on all islands. This interpretation is actually the most readily accepted one, given the morphological data. Despite the conventional treatment of these entities as two distinct species, their close morphological similarity could easily be interpreted as intraspecific variation. The present study emphasizes a critical need for genetic analysis of these species before further phylogenetic analysis is undertaken.

Scaevola mollis and *S. procera* appear as sister groups on the tree. This is noteworthy in that *S. procera* has been suggested to be a hybrid

derivative of *S. mollis* and *S. gaudichaudiana* (Gillett, 1966; Carlquist, 1969b). Removal of *S. procera* from the analysis does not alter the relationships among the other related species. Thus, although the data do not necessarily support a hybrid origin for *S. procera*, neither do they negate the possibility. Further field and genetic study is necessary before coming to conclusions about the role of hybridization in the origin of Hawaiian *Scaevola* species.

Results of the current analysis suggest that *Scaevola sericea*, common along coasts of essentially all Pacific islands, is the sister group to the diploid endemic species; however, it is morphologically distinct, and its fruit dispersal mechanism also points to strong differences between it and other species. *Scaevola sericea* is dispersed by buoyant fruits that are resistant to seawater, suggesting that this taxon arrived in the Hawaiian Islands in a different manner, hence at a different episode and in an independent colonization from the ancestor(s) of the endemic Pacific *Scaevola* species. Why the *S. sericea* lineage has not radiated as the diploid endemic lineage has remains unclear; however, the answer may be related to the dispersal and establishment ecology of *S. sericea* fruits. Van der Pijl (1972) pointed out that germination of these fruits occurs after a period of flotation in seawater followed by a washing in rainwater on land. This precise set of requirements may have prevented *S. sericea* from becoming established in more inland areas, limiting this species to beaches.

Adaptive Radiation in Hawaiian *Scaevola*

The overall phylogenetic pattern among the Hawaiian endemics is that radiation has proceeded from an ancestral lineage into clades that were adapted to different habitats, followed by subsequent speciation within mesic habitats but not by speciation within xeric habitats. This general pattern may be due to factors related to habitat type and the distribution of habitat types on different islands. However, the pattern may relate to inherent evolutionary plasticity within genetic lineages, irrespective of the habitat type in which various taxa occur.

The suggestion that the genus *Scaevola* has immigrated to the Hawaiian Islands during at least three different episodes is equivocal by the current phylogenetic analysis. An area cladogram for the species studied (Figure 16.3) offers information that can help explain the distributional patterns of *Scaevola*. There is a pattern of the older islands (Kaua'i, O'ahu, Moloka'i) supporting more wet-habitat species of *Scae-*

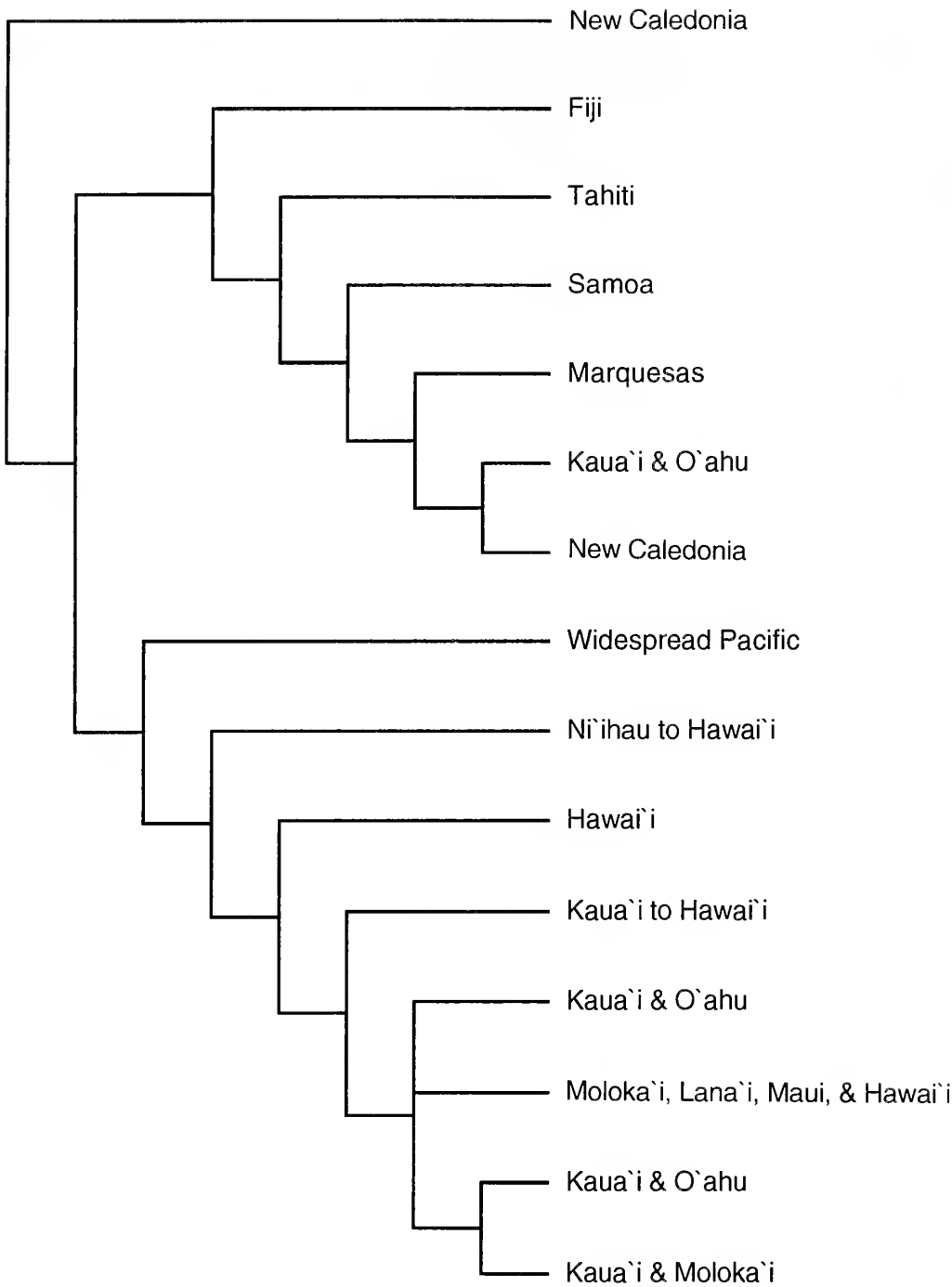


FIGURE 16.3. Area cladogram from the phylogenetic analyses for Pacific *Scaevola* species.

vola than younger islands. Moloka`i and O`ahu support three wet-forest species, and Kaua`i supports four. One explanation could be that the ancestor of the diploid lineage arrived on one of the older islands, after which adaptive radiation occurred. Subsequent dispersal of dry-habitat species such as *S. gaudichaudii* and *S. coriacea* to younger islands could have followed; however, wet-habitat species such as *S. mollis* and *S. pro-cera* apparently dispersed to a lesser extent. *Scaevola chamissoniana* may represent a derivative of *S. gaudichaudiana* that dispersed to younger islands. An implication that follows from this explanation is that pre-

sumed bird dispersers of dry-habitat species may be more effective than those of wet-habitat species.

Scaevola glabra occurs only on the two oldest islands in extremely wet habitats. Its more limited distribution may be related to its larger fruits that may be less likely to be transported longer distances by birds and perhaps also to extreme habitat requirements that may not be found on the younger islands.

Scaevola procera occurs on Kaua'i and Moloka'i but not O'ahu. Carlquist (1974) suggested the possibility of independent hybrid origins of *S. procera* on Kaua'i and Moloka'i. This explanation would be more attractive if the Moloka'i populations of *S. procera* were hybrids between *S. mollis* and *S. chamissoniana*, but this has not been suggested. Gillett (1966) found putative hybrids between *S. mollis* and *S. gaudichaudiana* on O'ahu, but they have not been referred to *S. procera*.

The area cladogram does not explain the distribution of *Scaevola kilaueae*. It is restricted in its range to the open dry shrubland on recent lava flows on the southeastern slopes of Kilauea. For whatever reason, this species has not expanded in range as have the other two arid-adapted species. This could be explained by greater dependence on certain habitat conditions, but little is known about the precise requirements of this species. There is also the possibility that it may be a relatively recently derived species that has not yet expanded its range.

Relationships and Biogeographic Patterns in Pacific *Scaevola*

The phylogeny obtained consistently places the non-Hawaiian Pacific *Scaevola* species in a position basal to the Hawaiian clade. This pattern suggests possible affinities among Pacific species but does not provide further clarification. For example, that *S. subcapitata* and *S. nubigena* are more closely related to each other than either is to *S. tahitiensis* is apparent from the cladogram, but additional conclusions are difficult to draw.

Endemic Pacific species of *Scaevola* have been postulated as having arrived on their respective islands via dispersal events; however, the number, sequence, and source of introductions have not been examined before. The base of the area cladogram for the Pacific *Scaevola* species under study (Figure 16.3) could be explained by sequential introductions into Fiji, Tahiti, Samoa, and the Marquesas Islands; however, the dispersal origin of these species on their respective islands constrains further speculation on the actual sequence or number of introductions. The

sequence of colonization implied by the phylogenetic analysis is not consistent in that Tahiti would have been colonized out of sequence in an eastward dispersal pattern.

Given the similarity in characters shared among the Pacific species, it is unlikely that morphological data alone can uncover further details of biogeographic patterns. The appearance of New Caledonia as a sister area to the Hawaiian Islands is curious. It could be explained by introduction of ancestors of Hawaiian species directly from New Caledonia, but the limited number of morphological characters plus the inclusion of only two New Caledonian species in this analysis prevents further speculation.

Another question that must be asked is to what extent extinction has had a role in producing the current patterns of *Scaevola* distribution in the Hawaiian and other Pacific islands. There are known records of populations of extant species becoming extinct (e.g., in *S. coriacea*); however, recent records of extinct populations are mostly due to human alteration of habitat, as is clearly the case in *S. coriacea*. Whether extinction not caused by humans has occurred in *Scaevola* remains uncertain.

CONCLUSION

The results of this study are limited by species that possess a highly homoplasious set of morphological characters, yet the information provided is provocative. It is evident that the Hawaiian diploid lineage is monophyletic and that within that lineage there is a distinction between dry- and wet-area species. It is also clear that *Scaevola sericea* represents a lineage distinct from the other Pacific species. The phylogeny is in accord with earlier claims that the Hawaiian species represent three distinct introductions. The likelihood that New Caledonia may support the most recent common ancestor to the Hawaiian taxa warrants further exploration. Results point to other patterns of relationships that can and should be tested using additional data. In particular, genetic studies in *Scaevola* are imperative before relationships are understood completely. Generation of molecular data sets can provide a much larger set of characters by which species can be examined phylogenetically.

ACKNOWLEDGMENTS

Thanks are due to the editors and anonymous reviewers for making critical suggestions about the manuscript. Warren L. Wagner generously

provided access to an unpublished manuscript on Marquesan *Scaevola* that furnished tremendous insight in this study. Amy David contributed the *Scaevola* illustrations.

APPENDIX 16.1. Character List for Pacific *Scaevola*

Multistate characters are treated as unordered.

1. Leaf surface: 0 = glabrous; 1 = hairy.
2. Leaf margins: 0 = entire; 1 = toothed.
3. Inflorescence type: 0 = compound thyrse; 1 = thyrse reduced to raceme above; 2 = raceme.
4. Pedicels: 0 = present; 1 = absent.
5. Bracteole type: 0 = similar to leaves but smaller; 1 = much smaller than leaves.
6. Calyx structure: 0 = sepals free; 1 = connate and lobed; 2 = forming a rim.
7. Sepal size: 0 = usually >1.5 mm; 1 = ≤1.5 mm.
8. Corolla lobe wings: 0 = present; 1 = absent.
9. Corolla texture: 0 = thick; 1 = thin.
10. Outer corolla hairs: 0 = absent; 1 = present.
11. Inner corolla hairs: 0 = present; 1 = absent.
12. Stamen length: 0 = same length as corolla tube; 1 = longer than corolla tube.
13. Anther hairs: 0 = absent; 1 = present.
14. Indusium upper surface: 0 = pubescent; 1 = glabrous.
15. Endocarp: 0 = smooth; 1 = rugose.

APPENDIX 16.2. Data Matrix of Character States for the Cladistic Analysis of Hawaiian and Related Pacific Species of *Scaevola*

The characters and character states are defined in Appendix 16.1. Missing data are indicated by question marks.

| OTU | Character | | | | | | | | | | | | | | |
|--------------------------|-----------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| <i>S. sericea</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>S. coriacea</i> | 0 | 0 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>S. gaudichaudii</i> | 0 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>S. gaudichaudiana</i> | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| <i>S. chamissoniana</i> | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>S. mollis</i> | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| <i>S. procera</i> | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| <i>S. kilaueae</i> | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| <i>S. glabra</i> | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| <i>S. montana</i> | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 |
| <i>S. coccinea</i> | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | ? | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>S. tahitiensis</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 |
| <i>S. subcapitata</i> | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| <i>S. floribunda</i> | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| <i>S. nubigena</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |

17

Biogeographic Patterns in the Hawaiian Islands

V. A. FUNK AND WARREN L. WAGNER

The Hawaiian Islands formed successively over a fixed geologic hot spot. The eight high islands (Ni'ihau, Kaua'i, O'ahu, Moloka'i, Lana'i, Kaho'olawe, Maui, and Hawai'i) occupy the southeast end of a long line of low islands and seamounts known as the Hawaiian Ridge and Emperor Chain. Carson and Clague have summarized the geologic history of the islands (see this volume, Chapter 2). In short, the oldest parts of the chain formed 75 to 80 million years ago (Ma) and the youngest are being formed today. The oldest of the high islands, Kaua'i, was formed ca. 5.1 Ma, and the youngest, Hawai'i, has three active volcanoes with the oldest flows formed no more than 0.5 Ma. Of major importance to the biogeographer were events that altered connections between certain volcanoes of the Hawaiian Islands during the Pleistocene. The most significant of these events was the breakup of a large island referred to as Maui Nui into the current islands of Moloka'i, Maui, Kaho'olawe, and Lana'i. O'ahu and Moloka'i were also connected by a low-elevation land bridge (see Carson and Clague, this volume, Chapter 2). The term *Maui Nui complex* is used to refer to two or more of the islands of Moloka'i, Maui, Lana'i, or Kaho'olawe, not necessarily to the giant island that existed in the Pleistocene.

The Hawaiian Islands are the most isolated major island group in the world. They have always been about as remote from all the continents as they are presently. Thus, the biota of the Hawaiian Islands is the result of dispersal from many different parts of the world, as is reflected by the

varied geographic ranges of the ancestors of the endemic plants and animals (Fosberg, 1948; Gressitt, 1963; Carlquist, 1974; Berger, 1981; Wagner et al., 1990). The sequential origin of the islands, coupled with their considerable size and isolation, makes the Hawaiian archipelago a unique place to investigate biological evolutionary history.

Because of their hot spot origin, the Hawaiian Islands are like a giant habitat conveyor belt. New volcanoes arise out of the ocean bare and available for any life that can reach them and survive. After the cessation of volcanic activity, the history of a volcanic island is one of constant erosion and subsidence. The wide sloping sides and alpine habitats of the young islands give way to the knife-edge ridges, steep slopes, and deep valleys of the older islands. Species that are specialized for the habitats of young volcanoes must move on to new volcanoes or give rise to species that can inhabit the new environment created by erosion and subsidence of older volcanoes. Eventually, an island erodes and subsides to a size where there are no longer alpine areas and wet forest, and only relatively dry coastal habitats remain.

Most multiple-island distributions are the result of dispersal between islands. However, vicariance patterns are possible within clades (monophyletic groups) or grades (paraphyletic groups) either on individual islands or among volcanoes that have been connected in the past, especially on Maui Nui. For instance, on each island that has more than one species of a lineage and whose species are the result of a single introduction, the intra-island pattern may be the result of vicariance. Erosion during the posteruptional stage of an island could dissect previously continuous species distribution into geographically discontinuous population mosaics. Another possibility for vicariance involves the four current islands that made up Maui Nui. A vicariant pattern resulting from the breakup of Maui Nui would not necessarily exhibit any correlation with island age. This would be the case in the separation and isolation of populations of a widespread species, followed by speciation in the isolates. Thus, absence of resolution on the area cladogram among the taxa of the islands that made up Maui Nui may be the result of vicariance. To document vicariance, repeating patterns must be detected within unrelated clades either within a single island or among the islands of the Maui Nui complex.

Using the phylogenies and area cladograms in this volume (Table 17.1), we seek to investigate the following questions: How many different biogeographic patterns were found? Are any of these patterns

TABLE 17.1. List of Genera and Lineages Discussed, and the Contributors

| Taxon | Contributor(s) |
|--|---|
| Insects | |
| Drosophilidae (fruit flies) | DeSalle; Kaneshiro et al. |
| <i>Laupala</i> (crickets) | Shaw |
| <i>Prognathogryllus</i> (crickets) | Shaw |
| <i>Sarona</i> (true bugs) | Asquith |
| Spiders | |
| <i>Tetragnatha</i> (spiders; two lineages) | Gillespie and Croom |
| Birds | |
| Drepanidinae (honeycreepers) | Tarr and Fleischer |
| Flowering plants | |
| <i>Clermontia</i> (Campanulaceae) | Lammers |
| <i>Cyanea</i> (Campanulaceae) | Givnish et al. |
| <i>Dubautia</i> , <i>Wilkesia</i> and <i>Argyroxiphium</i> (Asteraceae) | Baldwin and Robichaux; Funk and Wagner |
| <i>Geranium</i> (Geraniaceae) | Funk and Wagner |
| <i>Hesperomannia</i> (Asteraceae) | Funk and Wagner |
| <i>Hibiscadelphus</i> (Malvaceae) | Funk and Wagner |
| <i>Kokia</i> (Malvaceae) | Funk and Wagner |
| <i>Platydesma</i> (Rutaceae) | Funk and Wagner |
| <i>Remya</i> (Asteraceae) | Funk and Wagner |
| <i>Scaevola</i> (Goodeniaceae) | Patterson |
| <i>Schiedea</i> and <i>Alsinidendron</i> (Caryophyllaceae) | Wagner et al. |
| <i>Tetramolopium</i> (Asteraceae) | Lowrey |

consistent with one another? Are the patterns consistent with a priori hypothetical patterns? Is speciation generally inter- or intra-island?

The answers to these particular questions may provide insights for answering the more general question of whether the evolutionary history of the Hawaiian biota mirrors the geologic history of the islands.

METHODS

Standard phylogenetic methods were used to analyze the data for the 25 lineages presented in this volume. Kaneshiro et al. (Chapter 5) used species groups rather than individual species as the terminal taxa, and their results are less directly comparable with other studies in this volume.

An overview of the phylogenetic methodology is presented earlier in this volume (Chapter 3). For this chapter, the cladograms were generated using the computer program PAUP version 3.1.1 (Swofford, 1993). With a few minor exceptions, the cladograms produced were identical to those generated by the contributors; differences that were found did not affect any biogeographic conclusions. Individual cladograms were converted to area cladograms by replacing the terminal taxa with their geographic distribution.

To avoid ambiguity, we refer to the situation of multiple species making up a clade or grade on the same island as "intra-island radiation," or simply "radiation." Inter-island colonization is referred to as "dispersal."

Optimization was used to determine the island of origin of the ancestors of several lineages (Chapter 3). Although this method can be informative, it does have limitations and problems. For example, optimization designates the possible island of origin of the ancestor of the base of the extant clade; such information cannot be used to determine whether the lineage occurred earlier on an older, now-eroded island. There are also some instances in which optimization cannot give an answer, most notably when each island has only one species of a clade. Finally, species that have dispersed to other islands without speciation create problems for optimization by making it difficult to determine the island on which the speciation event took place. This problem is not restricted to optimization on island studies, because widespread species create problems for all biogeographic studies regardless of the method or location.

We established several hypothetical patterns that reflect the expected area cladogram for different presumed evolutionary histories. The actual area cladograms of the endemic lineages were compared with the hypothetical area cladograms to determine which, if any, of the hypothetical patterns were supported by the data. When originally formulating our hypothetical patterns, we underestimated the amount of intra-island radiation and therefore found it necessary to increase its importance by adding two patterns after the analysis began.

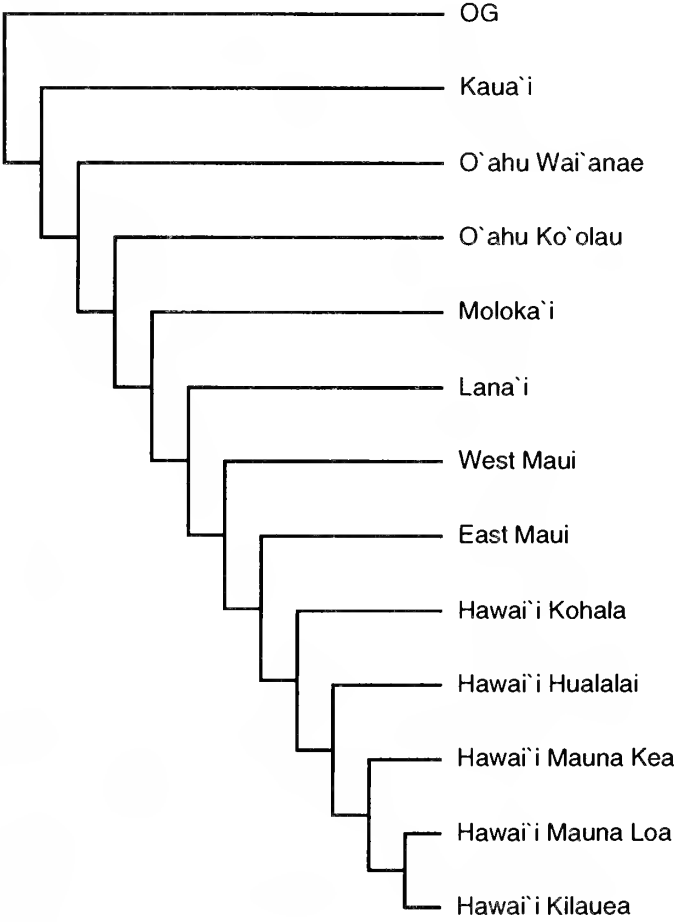
The hypothetical patterns can be divided into two basic groups: simple patterns and complex patterns. A subset of one complex pattern is discussed in more detail separately as younger island patterns. Basic attributes of the patterns and their accompanying evolutionary implications are described below.

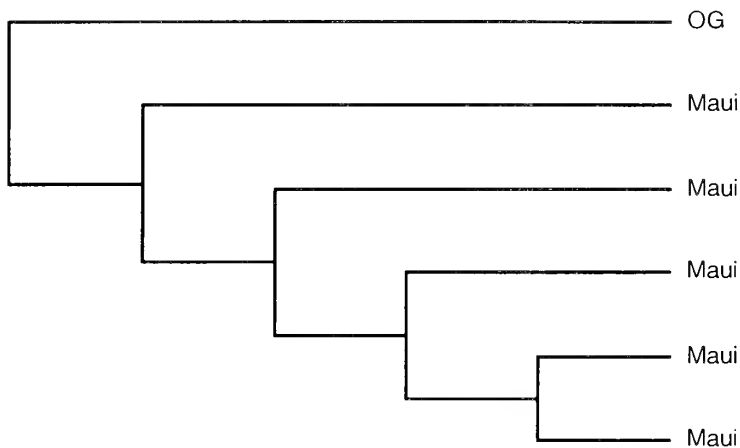
BASIC PATTERNS

Progression Rule

Previously the progression rule (Hennig, 1966; Wiley, 1981) was used to compare the cladogram and the distribution pattern and did not involve the geologic history of the area. As used here, it is necessary that the ancestor of the clade arrived on what is now the oldest high island, Kauaʻi, when it was young, either from outside the Hawaiian Islands or from an older, now-submerged or eroded island, and as each new volcano became available for colonization, a dispersal event associated with speciation occurred from the older to the younger volcano. The area cladogram resulting from this hypothesis is a ladderlike progression involving the volcanoes of the six main high islands (Figure 17.1). For any taxon, if only one species evolved on each successive volcano and if none of the species became widespread, then the area cladogram would be consistent with this pattern. Not all the islands have to be involved, but for those that are, the branching sequence on the area cladogram would be consistent with this pattern. If such an area cladogram were optimized for the distribution, the result would be inconclusive because there is only one species per volcano.

FIGURE 17.1. Hypothetical progression rule pattern. OG, outgroup.





Radiation

A taxon arrives and radiates on an island, thus all speciation is intra-island. If the original dispersal occurred on Maui and speciation occurred without any inter-island dispersal, then the pattern shown in Figure 17.2 would result.

Unresolved

An unresolved pattern (Figure 17.3) could be created in at least two ways: by repeated dispersal of a single species to several islands before any speciation, or by repeated dispersal from an older, now-severely eroded and subsided island by several members of the same clade with loss of all the unique identifying characters of those species. An unresolved pattern must be viewed with caution, however, because it could result from insufficient data to resolve the members of the clade.

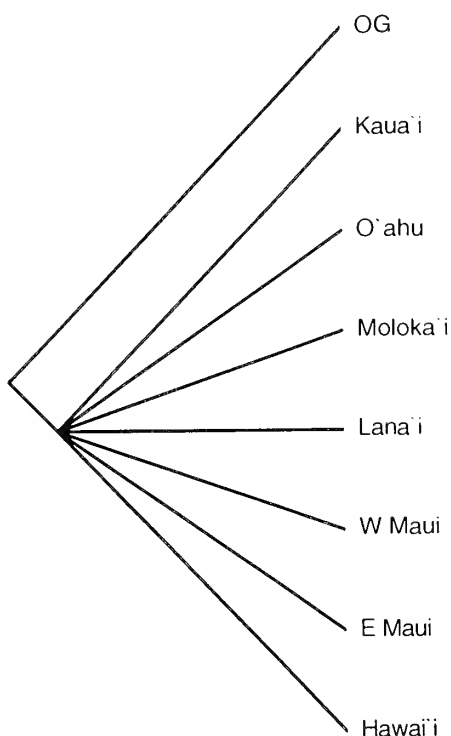
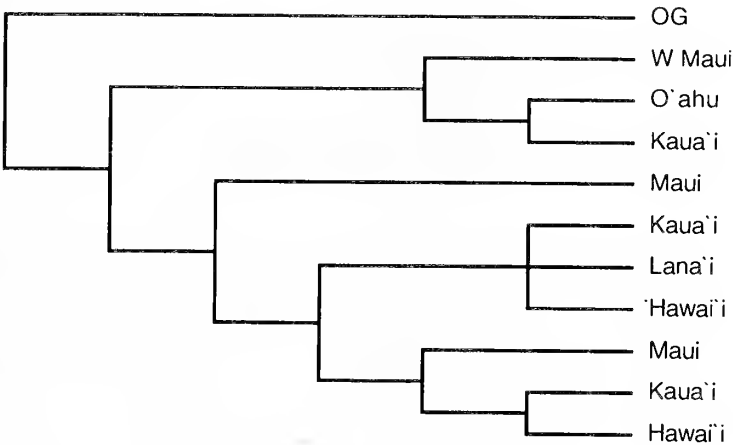


FIGURE 17.4. Hypothetical stochastic pattern. OG, outgroup.



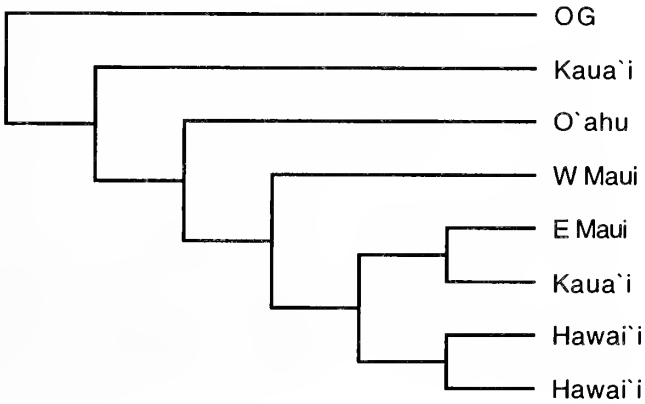
Stochastic

A cladogram of a lineage exhibiting a stochastic pattern would have a branching sequence, but the pattern of the area cladogram would not follow any known historical events. One explanation for this situation is that the species of a clade display extreme vagility, and the scale of their ability to colonize goes well beyond typical inter-island distances. Another explanation would entail random colonization and speciation; recency of introduction may also be a factor. A lineage that is relatively recent to the archipelago may be colonizing adjacent islands in a random fashion. The resulting area cladogram associated with any of these explanations would not have an obvious correlation with the geologic history of the islands. The clades presented in Figure 17.4 show examples of several possibilities for this scenario.

Back-Dispersal

An area cladogram of a lineage exhibiting back-dispersal would indicate that after a species is established on an island, it then disperses to an older island followed by speciation, in which case a progression pattern is interrupted. Such an event is illustrated in Figure 17.5, where a back-dispersal accompanied by speciation has taken place from East Maui to Kaua`i.

FIGURE 17.5. Hypothetical back-dispersal pattern. The example illustrates a back-dispersal from East Maui to Kaua`i. OG, outgroup.



COMBINED PATTERNS

Progressive Clades and Grades

If a lineage has multiple species on one or more islands resulting from a single introduction, the area cladogram can consist of clades (Figure 17.6), grades (Figure 17.7), or various combinations of the two. What topologies can be formed depends on the position in the evolutionary history of the group occupied by the inter-island colonist. Figures 17.8A, 17.9A, and 17.10A show radiation of the same taxa on the same three islands, each clade of nine species representing the species of an endemic genus. Different cladograms (Figures 17.8B, 17.9B, and 17.10B) and area cladograms (Figures 17.8C, 17.9C, 17.10C) are produced, depending on which taxon (from different phylogenetic positions of the clade) is the colonist to the new island. If dispersal to a new island occurs early in the evolutionary history of an extant clade (Figure 17.8A), the result is a progressive clade pattern (Figure 17.8B and C). In contrast, Figure 17.9A shows a colonist from a terminal taxon of the extant clade, so the cladogram (Figure 17.9B) and the area cladogram (Figure 17.9C) are ladderlike, forming progressive grades, except for the clade on the island

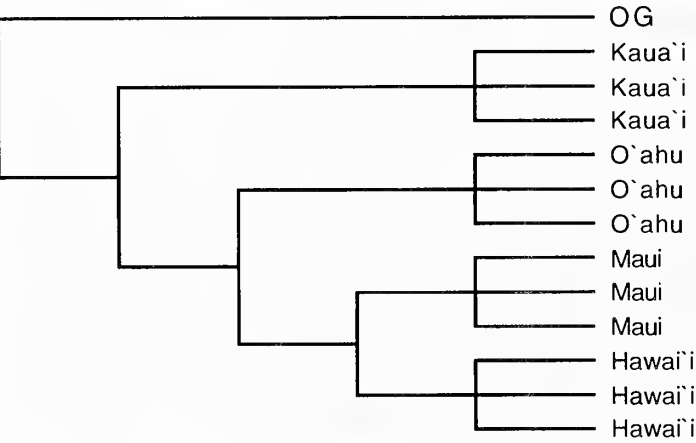


FIGURE 17.6. Hypothetical progressive clades pattern. OG, outgroup.

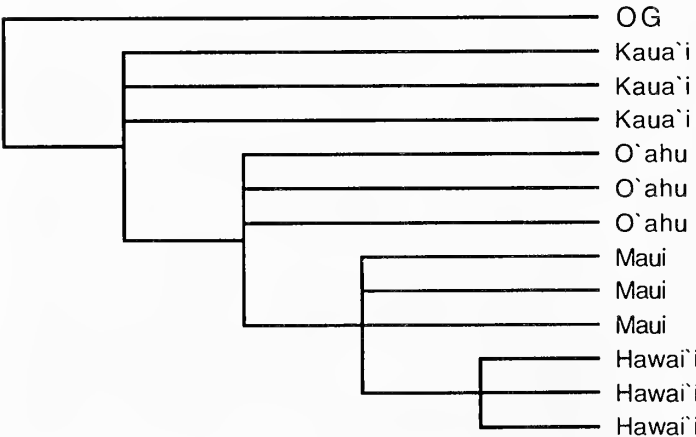


FIGURE 17.7. Hypothetical progressive grades pattern. OG, outgroup.

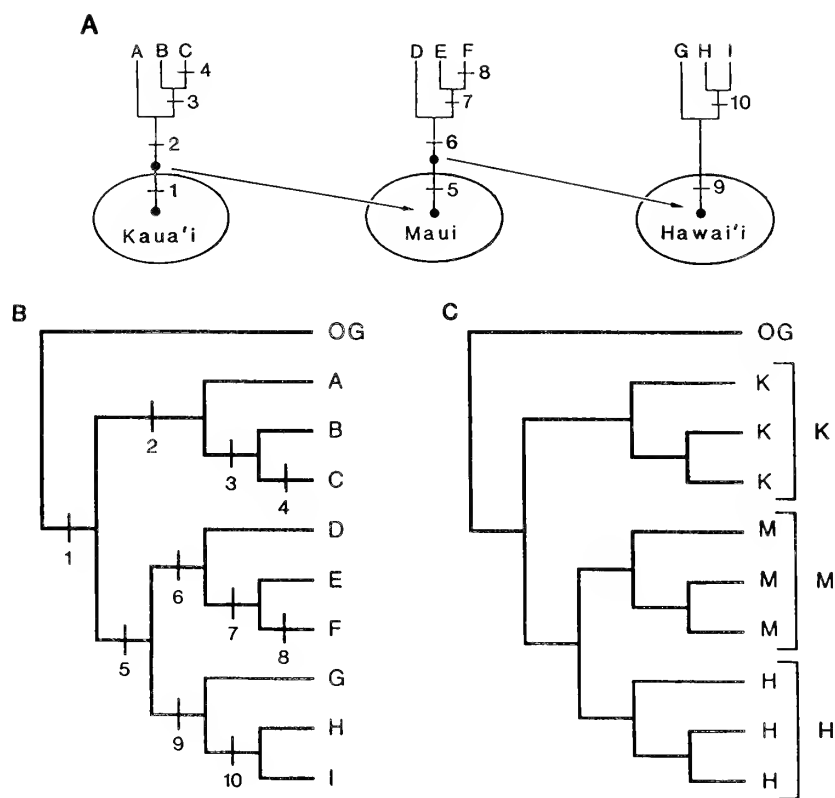


FIGURE 17.8. Hypothetical inter- and intra-island radiation that would produce a progressive clades pattern. (A) Schematic illustration of radiation; (B) cladogram for the schematic; (C) corresponding area cladogram. OG, outgroup; K, Kaua'i; M, Maui; H, Hawai'i.

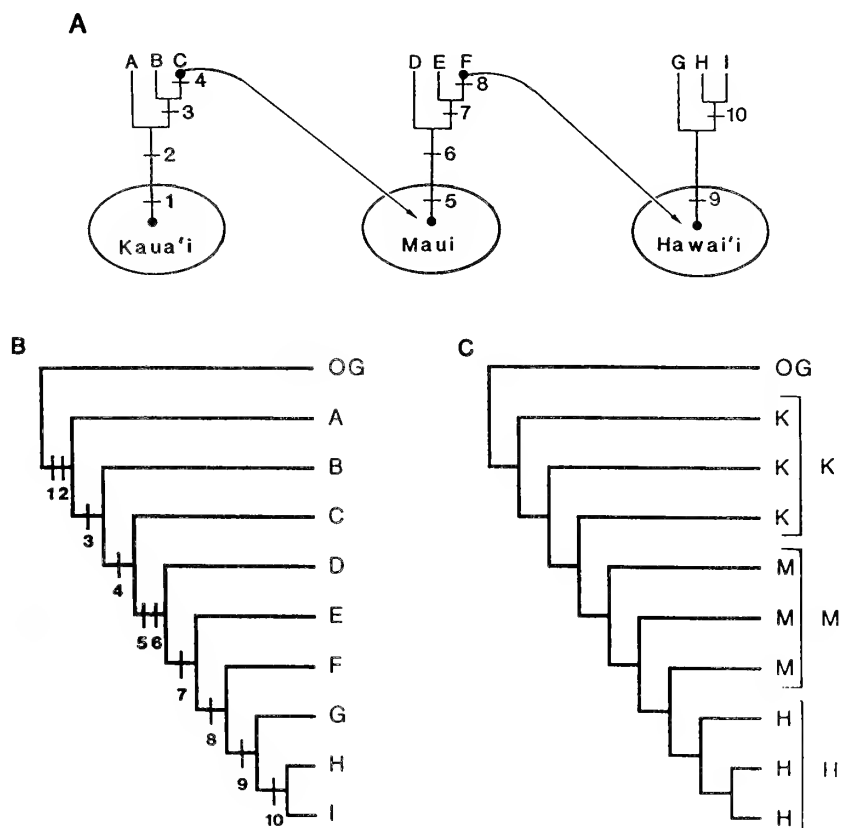


FIGURE 17.9. Hypothetical inter- and intra-island radiation that would produce a progressive grades pattern. (A) Schematic illustration of radiation; (B) cladogram for the schematic; (C) corresponding area cladogram. OG, outgroup; K, Kaua'i; M, Maui; H, Hawai'i.

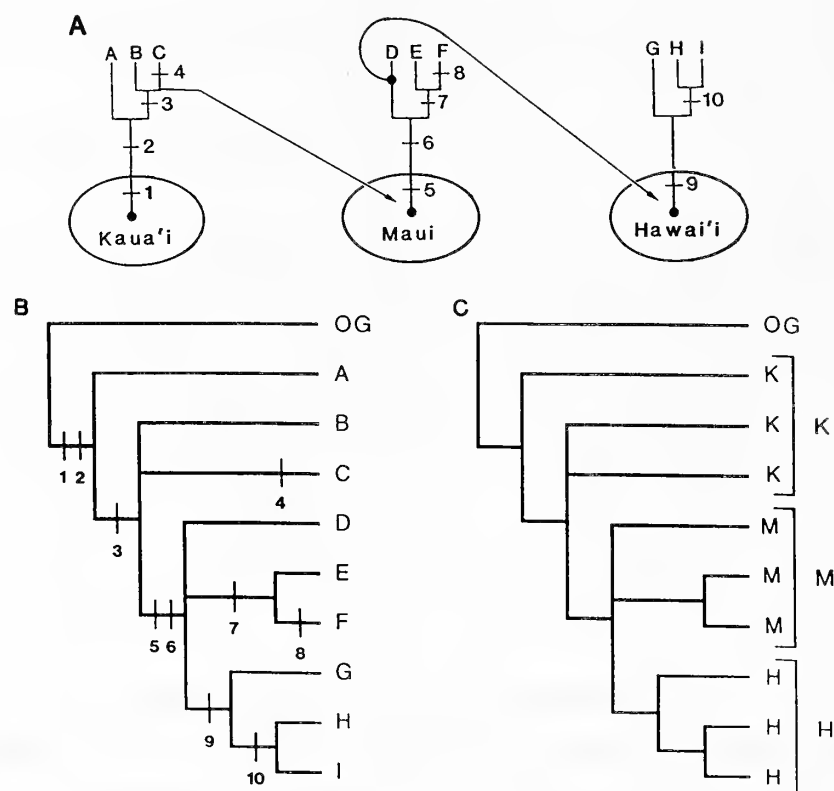


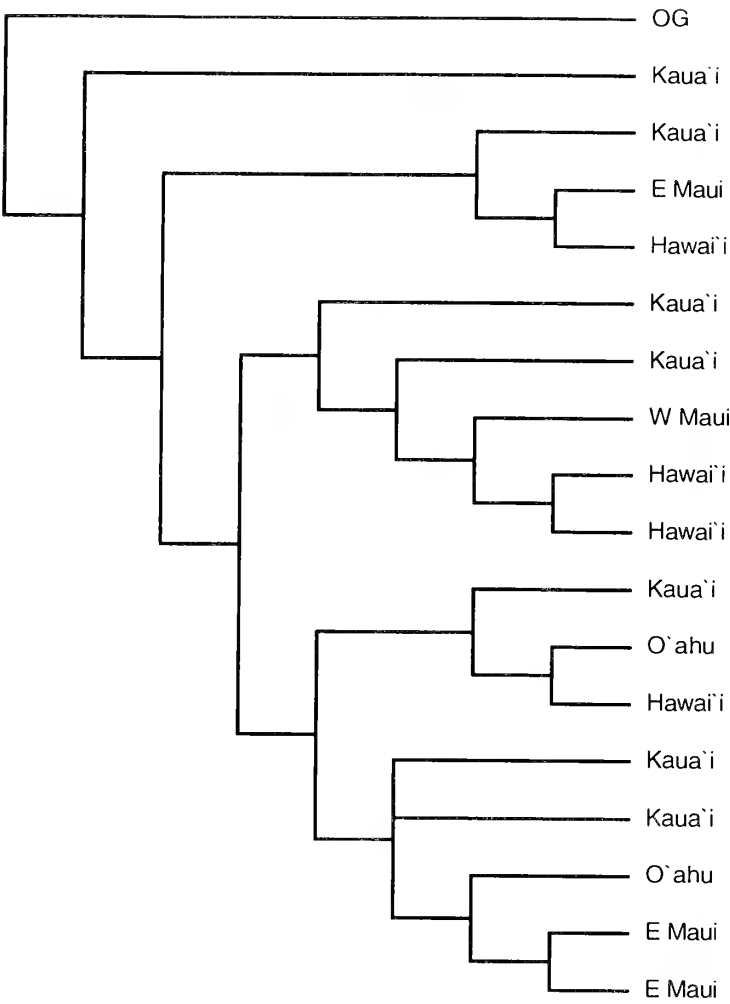
FIGURE 17.10. Hypothetical inter- and intra-island radiation that would produce a mixed pattern. (A) Schematic illustration of radiation; (B) cladogram for the schematic; (C) corresponding area cladogram. OG, outgroup; K, Kaua'i; M, Maui; H, Hawai'i.

of Hawai'i, which has not dispersed to a new island. The colonists in Figure 17.10A are from two different intermediate positions in the clade, and the resulting cladogram (Figure 17.10B) and area cladogram (Figure 17.10C) are a combination of clades, grades, and unresolved nodes. Although a wide variety of patterns is possible, all share a common feature in that species from a particular island are grouped together in a clade or grade, and the overall pattern of the area cladogram is consistent with the progression rule. Although there is speciation within and between islands, the overall pattern is one of progression from oldest to youngest island within a lineage. In the next combined pattern, the overall inter-island pattern is not so obvious.

Terminal Resolution

A terminal resolution pattern exhibits several well-defined clades as subpatterns and either an unresolved base or a base that has experienced a radiation on an older island. The subpatterns are either progressions or radiations. Both of these possibilities indicate repeated introductions from an older, now-severely eroded or submerged island. The first,

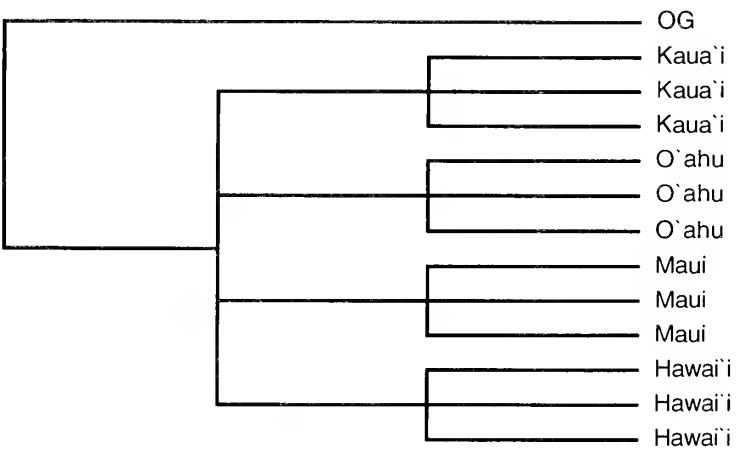
FIGURE 17.11. Hypothetical terminal resolution pattern with an overall pattern of radiation; the subpatterns are progressions. OG, outgroup.



shown in Figure 17.11, exhibits a grade as the basic pattern, indicating that the origin of the clade is a radiation on that island (in this case, Kaua'i) or that the ancestors of the extant species dispersed from an older island and the descendent species have retained enough of the characters of their ancestors to preserve the relationship structure of the cladogram. In Figure 17.11, the subpatterns are progressions, but some could involve radiations.

The second case is shown in Figure 17.12. It demonstrates an unresolved base, indicating that the lineage experienced repeated dispers-

FIGURE 17.12. Hypothetical terminal resolution with an overall pattern that is unresolved; the subpatterns are radiations. OG, outgroup.



als from the same or a very similar ancestor or that the characters that separated the ancestral species from one another have been lost. Although the colonists to the current high islands from now-submerged or severely eroded older islands were not necessarily from the same species, they were all members of the same lineage, and because the ancestors are now extinct, the lineage is now a single clade. In Figure 17.12, the subpatterns are radiations, but they could also be progressions.

Most of the patterns described above reflect evolutionary scenarios that depict an older-to-younger island colonization. There also are patterns that center on younger islands. These have different interpretations than those involving colonization from older to younger islands.

YOUNGER ISLAND PATTERNS

Recent Colonization

If a taxon arrived in the Hawaiian Islands directly onto one of the current eight high islands while that island was young, the resulting pattern might reflect a combination of dispersal events from younger to older islands in a random or unresolved pattern and, at the same time, develop a ladderlike progression for species that arise as new islands emerge. Figure 17.13 shows results of a colonization on East Maui when it was the youngest island in the chain. After successful colonization, the species dispersed to Moloka'i. It also underwent radiation on East Maui, with one species dispersing to O'ahu and another eventually dispersing to Hawai'i to form a progression for the terminal three species of the lineage. If speciation occurred on East Maui before any dispersal, the taxa resulting from the dispersal events to the older islands would be nested within the East Maui clade. By contrast, if the colonist were a recent

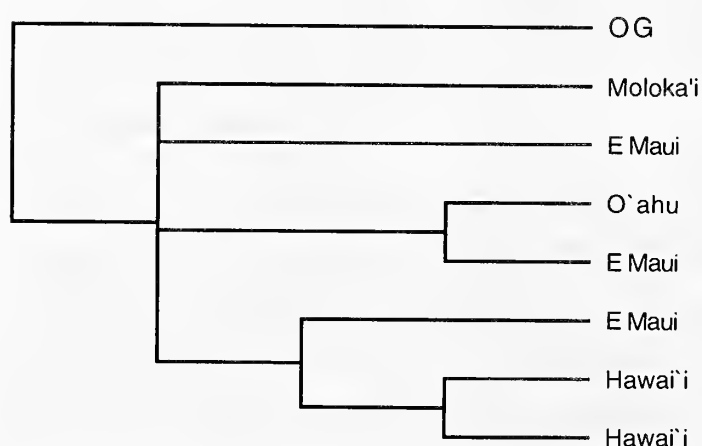


FIGURE 17.13. Hypothetical younger island pattern showing recent colonization. OG, outgroup.

arrival, there would be only the dispersal part of the area cladogram mentioned above.

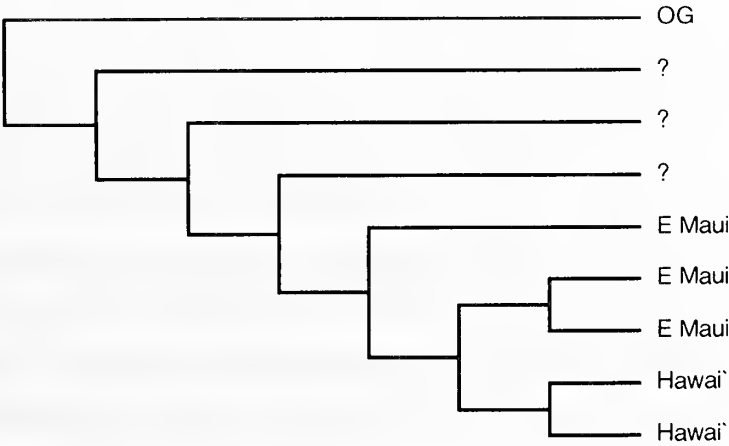
Extinction

If a taxon is specific to habitats found only on younger islands, the loss of such habitats with erosion and subsidence on increasingly older islands would cause the diversity of the area cladogram to shift continually to the younger islands. As a result, area cladograms could be either progressions or radiations but would not include any of the older islands even though the lineage was once present on these islands (Figure 17.14). Can this pattern be distinguished from one of a clade that colonized one of the younger islands and has not back-dispersed along the chain?

One way to differentiate between these two patterns is to assess the amount of change that has taken place between the Hawaiian lineage and the most closely related group outside the archipelago. East Maui was formed only 0.75 Ma, so if a lineage had its origin on East Maui, all the observed diversity would have evolved less than 0.75 Ma. Another way to differentiate between these two patterns would be to examine the geographic occurrences of the habitats to which the species of the lineage are restricted. For example, subalpine and young lava flow habitats have been lost on the older islands, presumably along with any species associated with these environments. Some consideration should be given to the likelihood of an extinction pattern in any lineage restricted to young islands.

The patterns described in the above section were designed to predict the type of area cladogram that would result if certain types of evolutionary histories had occurred. The actual cladograms from the other chapters must be compared with the hypothetical ones to determine if any of the latter are supported.

FIGURE 17.14. Hypothetical younger island pattern showing extinction in the basal taxa of the lineage, with extinction indicated by a *question mark*. OG, out-group.



SEARCH FOR COMMON PATTERNS

This section examines the results of each data chapter included in this volume. To directly compare the phylogenetic information relevant to biogeographic interpretations from the various chapters, we present an area cladogram for each lineage in a uniform style without any extraneous information other than the branching sequence. We begin with the simplest of the area cladograms and move to the increasingly more complex examples. A question mark on a figure usually indicates there is more than one equally parsimonious way to distribute the islands at that point on the area cladogram. An asterisk indicates that a particular group of taxa forms a grade on the area cladogram; all other groups are indicated monophyletic. Colonization patterns are indicated in the text by island abbreviations (K, Kaua'i; O, O'ahu; Mo, Moloka'i; L, Lana'i; EM, East Maui; WM, West Maui; M, Maui; MN, the Maui Nui complex; H, Hawai'i) connected by an arrow indicating direction of colonization.

Hawaiian Drosophilidae (Kaneshiro, Chapter 5; DeSalle, Chapter 6)

The general area cladogram of the sampled *Drosophila* lineages by DeSalle (Chapter 6) exhibits the progression rule pattern. Moreover, the analysis showed that each of the six clades (Figure 17.15) were consistent with the progression rule pattern with a few progressive clades and grades and that all were consistent with an overall pattern of colonization from older to younger islands (O → Mo → WM → EM → H) following the progression rule. Because each of the sublineages is a part of the larger Drosophilidae clade, there is an overall pattern to consider. We do not know how all these clades in the Hawaiian Islands are related to each other; however, it seems likely that the overall pattern would be terminal resolution because the subpatterns of component lineages represent progressions.

The Drosophilidae were also discussed by Kaneshiro et al. (Chapter 5). Because the terminal taxa in their study were species groups rather than individual species, it is difficult to compare the results here. However, most of the *Drosophila* clades have members on two or more islands, and the biogeographic pattern is consistent with the results of DeSalle's analyses in that each lineage of flies he examined had an inter-island distribution pattern, rather than a radiation on a single island. Among the 29 terminal taxa in Kaneshiro's cladogram, only 6 of the nonbasal ones have species on Kaua'i. This also agrees with DeSalle's findings; all six of his clades were distributed from O'ahu to the younger

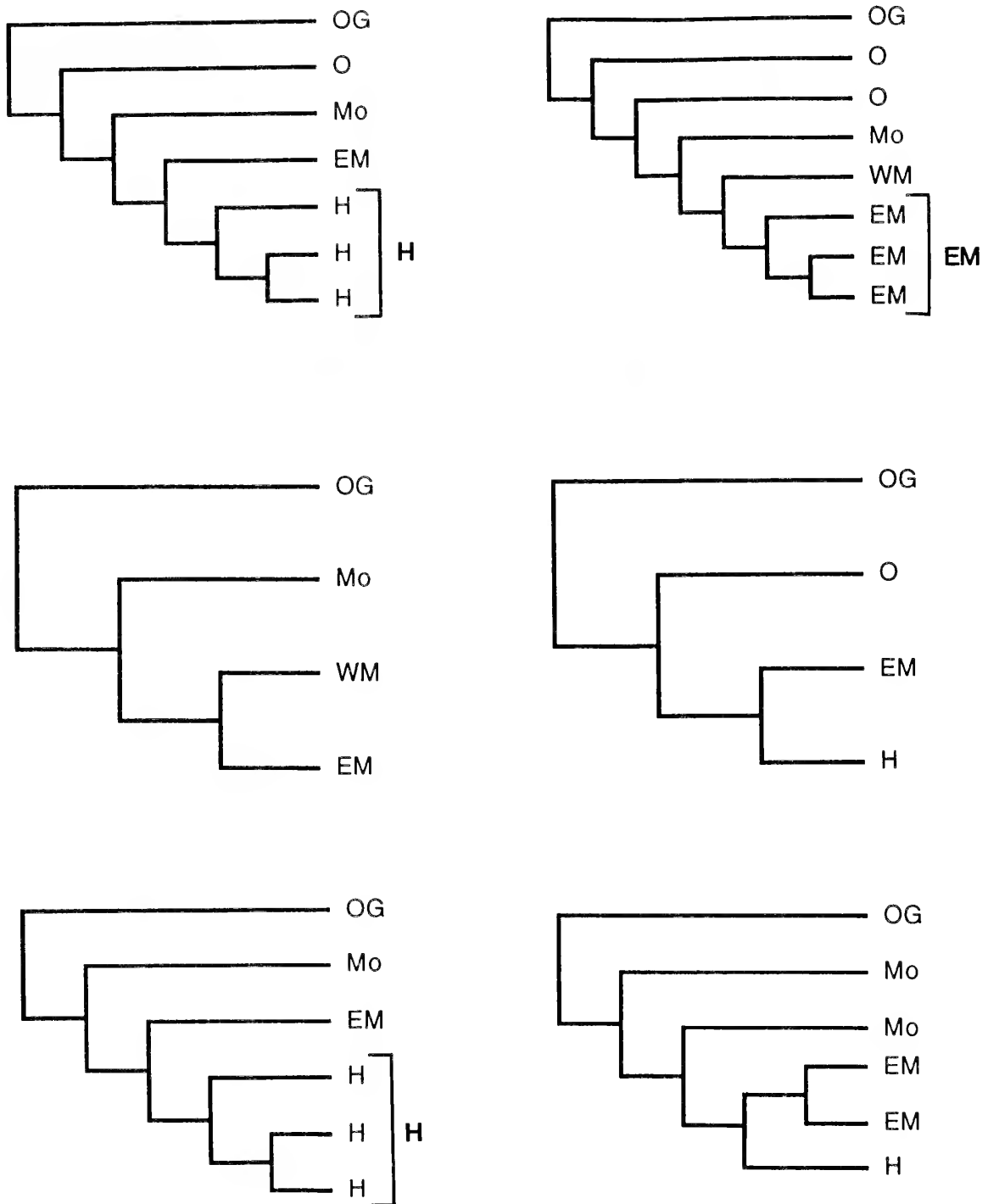


FIGURE 17.15. Area cladograms for the six clades of Hawaiian *Drosophila* data from DeSalle (Chapter 6). OG, outgroup; O, O'ahu; Mo, Moloka'i; WM, West Maui; M, Maui; EM, East Maui; H, Hawai'i.

islands, and none of them had species on Kaua'i. Three of the basal groups, however, occur on Kaua'i, so when the area cladogram is optimized, it gives a Kaua'i ancestor for the entire clade.

Remya, *Hesperomannia*, and *Kokia* (Funk and Wagner, Chapter 10)

Remya and *Hesperomannia* are small Asteraceae genera that exhibit patterns consistent with the progression rule (Figure 17.16A and B). A

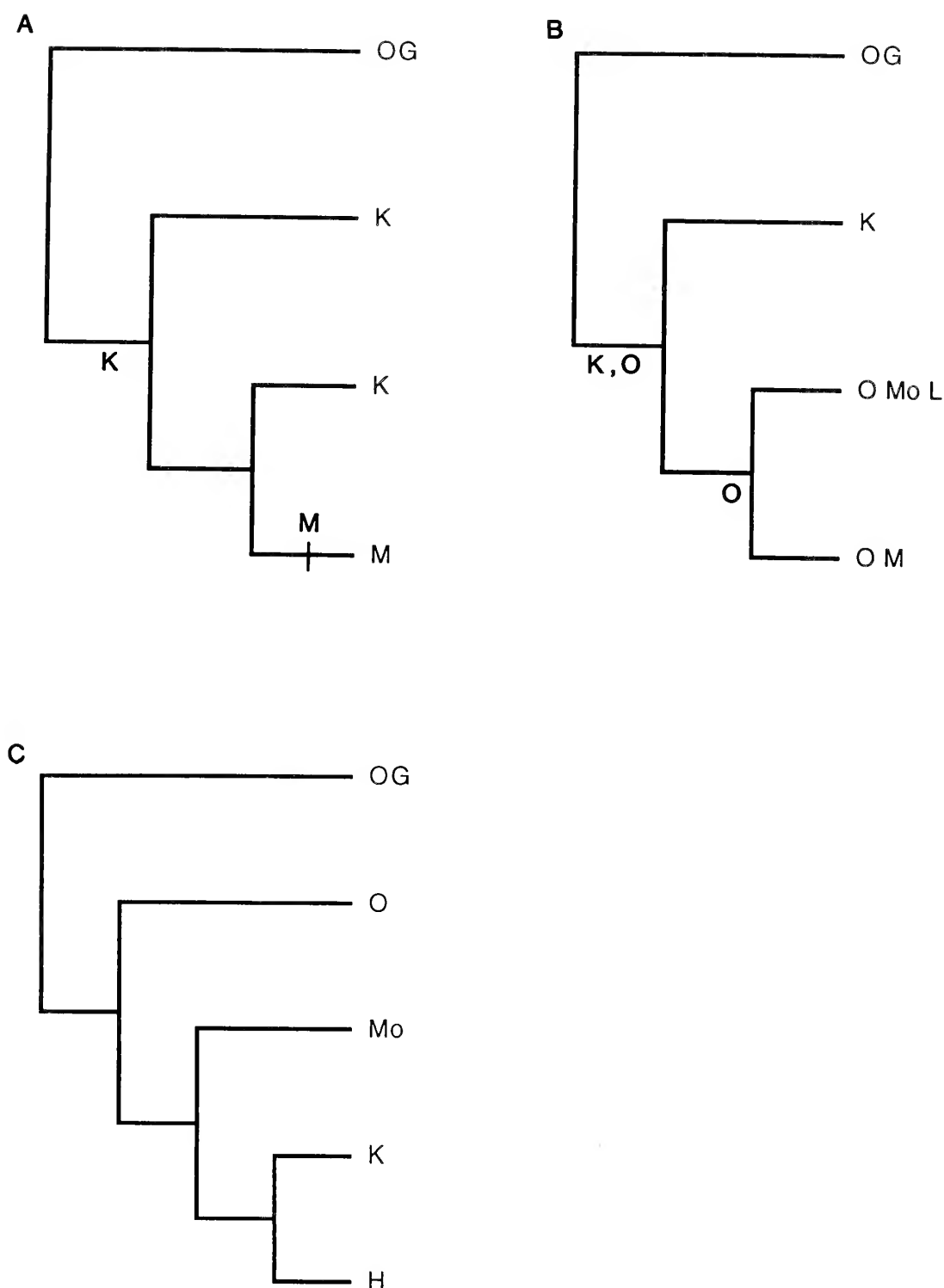
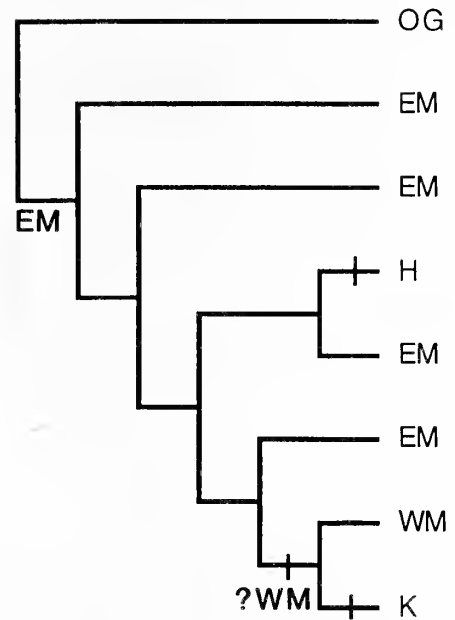


FIGURE 17.16. Area cladograms for three genera of flowering plants, data from Funk and Wagner (Chapter 10). (A) *Remya*; (B) *Hesperomannia*; (C) *Kokia*. OG, outgroup; K, Kaua'i; O, O'ahu; Mo, Moloka'i; L, Lana'i; M, Maui; H, Hawai'i.

Kaua'i ancestor is unambiguously indicated for *Remya*, whereas the situation in *Hesperomannia* is equivocal, with either a Kaua'i or an O'ahu ancestor. The area cladogram of *Kokia* (Malvaceae) (Figure 17.16C) is more complicated. It is consistent with two patterns: The overall pattern is compatible with the progression rule, with the compounding hypothesis

FIGURE 17.17. Area cladogram for *Geranium* section *Neurophyllodes*, data from Funk and Wagner (Chapter 10). It is equally parsimonious to hypothesize a Kaua'i or West Maui origin for the terminal two-taxa clade, indicated by the *question mark*. OG, outgroup; K, Kaua'i; WM, West Maui; EM, East Maui; H, Hawai'i.



of a single back-dispersal to Kaua'i. As mentioned earlier, and as demonstrated with *Drosophila* and *Kokia*, optimization is not an effective tool when there is only one species per island.

Geranium Section *Neurophyllodes* (Funk and Wagner, Chapter 10)

The endemic Hawaiian geraniums show a radiation pattern with the clade on East Maui (Figure 17.17). Most of the speciation events are associated with the radiation, but three dispersal events are associated with speciation, involving a dispersal to Hawai'i (progression rule) and two cases of back-dispersal, one each to Kaua'i and West Maui. The Hawaiian shrubby *Geranium* lineage is well defined and unique in many ways from extra-Hawaiian *Geranium*. Because the basal Hawaiian species occur in subalpine habitats, this lineage may represent an example of habitat loss and associated extinction so that although the current clade apparently originated on East Maui, the age of the lineage in the archipelago could be much older, in which case now-extinct species would have existed on islands that once had subalpine habitat.

Drepanidinae (Tarr and Fleischer, Chapter 9)

The area cladogram of the honeycreeper species that were sampled shows an equivocal base of either Maui or Kaua'i (Figure 17.18). However, the position of the basal taxon on the cladogram is in doubt (see Tarr and Fleischer, this volume, Chapter 9). Leaving out this basal taxon and starting one branch up from the base, the distribution shows a Kaua'i origin and radiation followed by dispersal to other islands. However, not

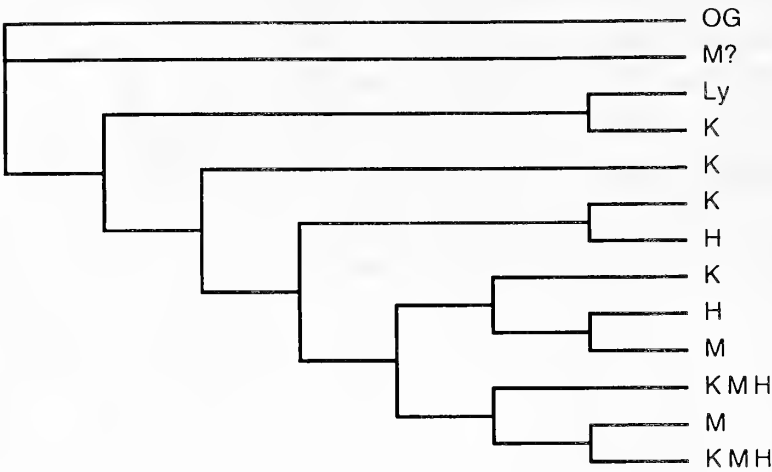


FIGURE 17.18. Area cladogram for some species of the Hawaiian Drepanidinae, data from Tarr and Fleischer (Chapter 9). OG, outgroup; Ly, Laysan; K, Kaua'i; M, Maui; H, Hawai'i; the *question mark* indicates that the placement of this taxon is in question.

all the extant honeycreeper taxa have been included in the study. Furthermore, several additional species of *Telespiza* from Kaua'i, O'ahu, Moloka'i, and Maui are known only from fossils (Olson and James, 1982b; James and Olson, 1991). This shows that many honeycreeper taxa were once more widespread and that the vagility of the honeycreeper lineage exceeds that of most of the other taxa considered in this volume. Their area of easy dispersal is great enough that the scale on which they differentiate geographically exceeds the inter-island distances between the Hawaiian volcanoes, creating a stochastic pattern.

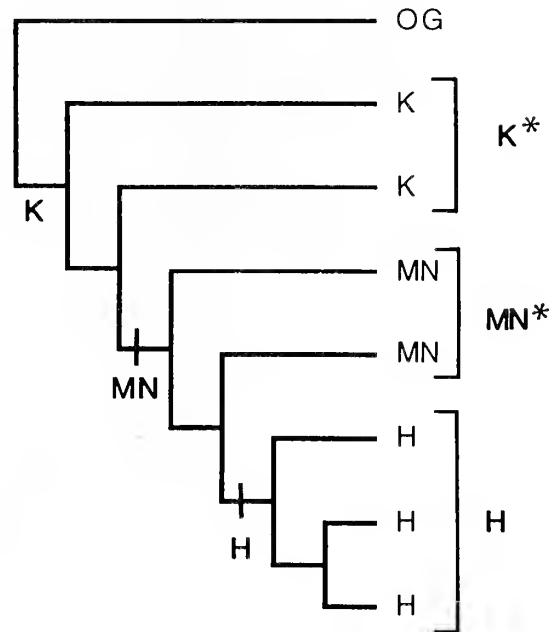
***Hibiscadelphus* (Funk and Wagner, Chapter 10)**

The area cladogram for *Hibiscadelphus* (Figure 17.19) shows a basic progressive clades and grades pattern, with a two-taxa grade on both Kaua'i and the Maui Nui complex and a terminal clade on the island of Hawai'i. When the distribution is optimized on the cladogram, it indicates a Kaua'i ancestor for the clade and an inter-island dispersal pattern of K → MN → H.

***Prognathogryllus* and *Laupala* (Shaw, Chapter 4)**

The two area cladograms of crickets have different specific patterns, but they are of the same type. The first one, for *Prognathogryllus* (Fig-

FIGURE 17.19. Area cladogram for *Hibiscadelphus*, data from Funk and Wagner (Chapter 10). OG, outgroup; K, Kaua'i; MN, Maui Nui complex; H, Hawai'i; an *asterisk* denotes a group of taxa that form a grade, and all other groups are clades.



ure 17.20), exhibits an overall pattern of progressive clades and grades. Progressive clades and grades are on Kaua'i and O'ahu, followed by two sister clades; one indicates a radiation on Hawai'i with a back-dispersal to O'ahu, whereas the other suggests a radiation on Maui with a dispersal to Hawai'i and a back-dispersal to O'ahu. When the distribution is optimized on the area cladogram, a Kaua'i ancestor and a $K \rightarrow O \rightarrow M \rightarrow H$ dispersal pattern are indicated. The second genus, *Laupala* (Figure 17.21), also shows a combination of progressive clades and grades with radiation patterns on Kaua'i, O'ahu, Maui, and Hawai'i. However, when optimized one dispersal pattern is from $K \rightarrow O$, whereas the other is a $K \rightarrow M \rightarrow H$. In the Hawai'i clade, there are two cases of back-dispersal to Maui. The overall colonization pattern of both genera is dispersal from older to younger islands.

Hawaiian *Tetragnatha* (Gillespie and Croom, Chapter 8)

Two separate lineages of *Tetragnatha* were studied. The area cladograms appear somewhat different from those of Gillespie and Croom only because in this analysis subspecific taxa were combined so that all terminal taxa were species. The actual branching sequence for the species is identical to that in Gillespie and Croom. The area cladogram of the *elongate* clade (Figure 17.22) shows a progressive clades and grades pattern, with a grade on the Maui Nui complex and a clade on Hawai'i. This is followed by a back-dispersal pattern with dispersal from the island of Hawai'i clade to Kaua'i and East Maui. The overall pattern of coloni-

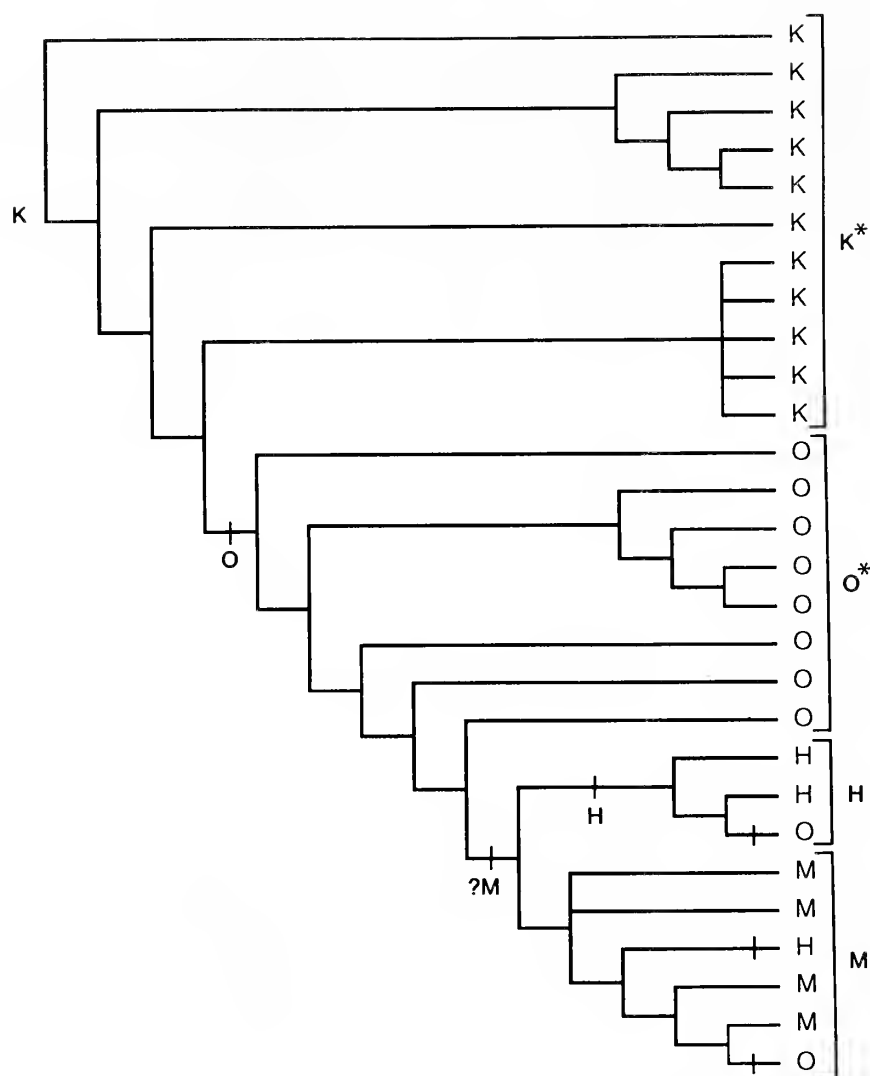


FIGURE 17.20. Area cladogram for *Prognathogryllus*, data from Shaw (Chapter 4). There are three equally parsimonious ways to arrange the areas for the two terminal clades. The one illustrated agrees with the progression rule. K, Kaua'i; O, O'ahu; M, Maui; H, Hawai'i; the *question mark* indicates there is more than one equally parsimonious way to distribute the islands at that point on the area cladogram; an *asterisk* denotes a group of taxa that form a grade, and all other groups are clades.

zation is $K \rightarrow MN \rightarrow H$, which is consistent with the older-to-younger island sequence. There is also some indication of a vicariant pattern for some taxa within the Maui Nui complex.

The patterns of the two sister clades of the *Tetragnatha spiny leg* lineage are less obvious than that of the *elongate* clade mentioned above. Both of the *spiny leg* clades show a basal group on Kaua'i and a clade that radiated on Maui and are therefore consistent with the progression rule, older-to-younger island pattern. One *spiny leg* clade (Figure 17.23A) is consistent with a $K \rightarrow EM$ dispersal pattern with two independent cases

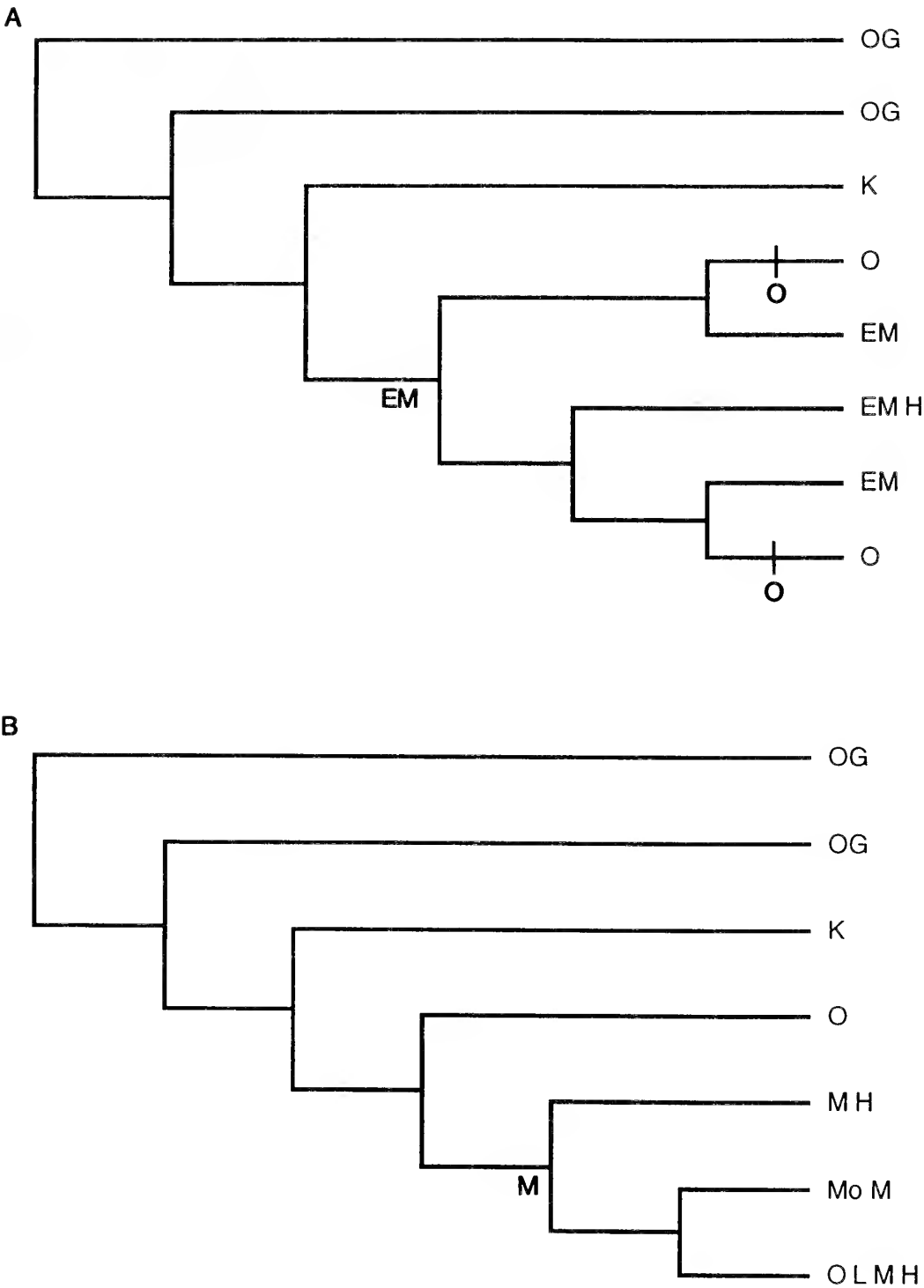


FIGURE 17.23. Area cladograms for *Tetraglatha*, data from Gillespie and Croom (Chapter 8). (A) *Spiny leg* clade 1; (B) *spiny leg* clade 2. OG, outgroup; K, Kaua‘i; O, O‘ahu; Mo, Moloka‘i; L, Lana‘i; M, Maui; EM, East Maui; H, Hawai‘i.

the group consisting of *Wilkesia* and *Dubautia*. As a result, the island of origin of the silversword alliance is unambiguously Kaua‘i based on the morphology data, whereas it is either Kaua‘i or Maui based on the molecular data. Based solely on the molecular area cladogram, a Kaua‘i or older island origin for the group is still preferred by Baldwin and Robichaux (Chapter 13). The morphology area cladogram exhibits a

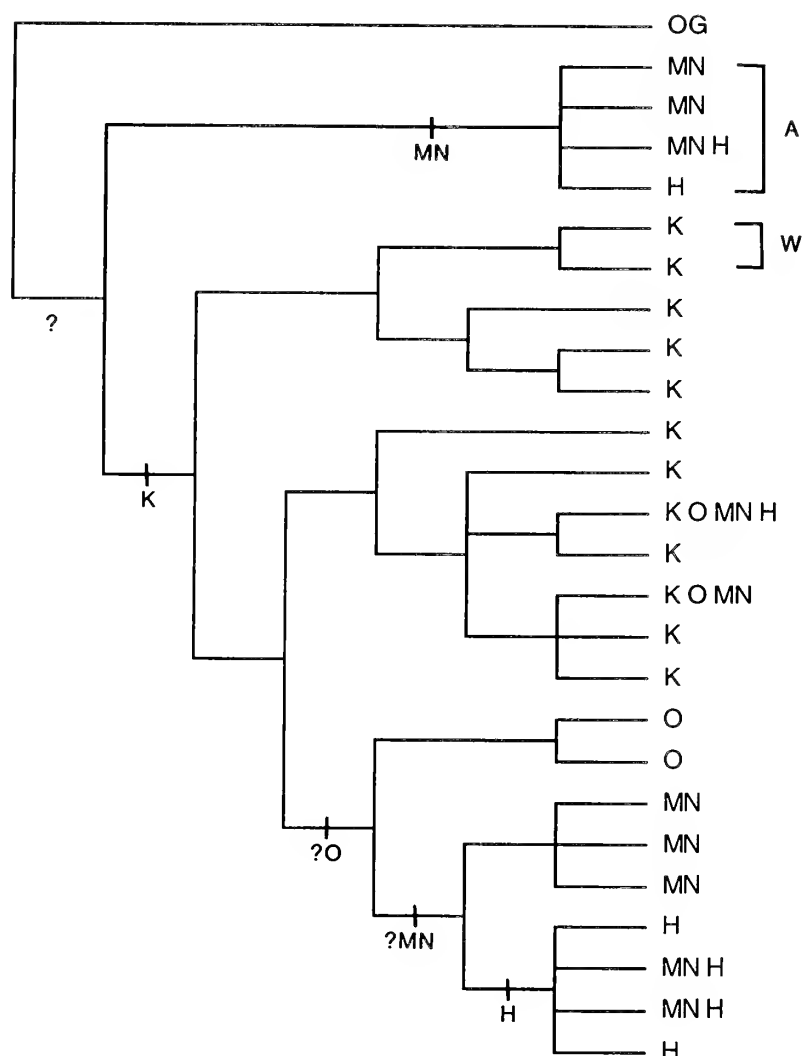
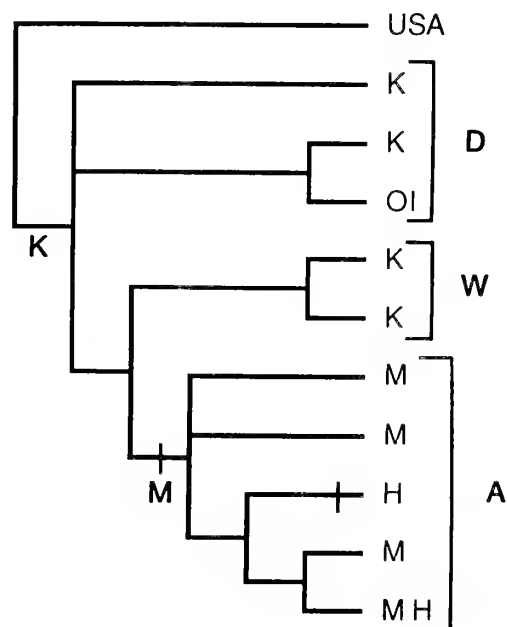


FIGURE 17.24. Area cladogram for the silversword alliance based on molecular data from Baldwin and Robichaux (Chapter 13). A, *Argyroxiphium*; W, *Wilkesia*; all remaining taxa are species of *Dubautia*. OG, outgroup; K, Kaua'i; O, O'ahu; MN, Maui Nui complex; H, Hawai'i; a *question mark* indicates there is more than one equally parsimonious way to distribute the islands at that point on the area cladogram.

FIGURE 17.25. Area cladogram for the silversword alliance based on morphological data from Funk and Wagner (Chapter 10). USA, continental United States (out-group); A, *Argyroxiphium*; D, *Dubautia*; W, *Wilkesia*; OI, islands other than Kaua'i; K, Kaua'i; M, Maui; H, Hawai'i.



progressive clades and grades pattern, including two radiations, one on Kaua‘i in *Wilkesia* and one on East Maui in *Argyroxiphium*.

In the molecular area cladogram, one can separate *Argyroxiphium* and the remainder of the area cladogram, producing two different patterns. The *Dubautia* and *Wilkesia* clade shows a definite progressive clades and grades pattern with a Kaua‘i base and an overall pattern consistent with a $K \rightarrow O \rightarrow MN \rightarrow H$ dispersal pattern. *Argyroxiphium*, however, expresses a radiation pattern, with Maui as its base. *Argyroxiphium* is confined to habitats that do not exist on any of the older islands; thus, like *Geranium*, *Argyroxiphium* may be an example of an extinction pattern. Like the morphological data, the molecular data show a Kaua‘i radiation for *Wilkesia* and an East Maui radiation for *Argyroxiphium*.

Schiedea and *Alsinidendron* (Wagner et al., Chapter 12)

Although there were six equally parsimonious trees, the differences among them involved minor changes that did not alter the biogeographic analysis. The area cladograms indicate a Kaua‘i origin for three of the extant *Schiedea* and *Alsinidendron* clades with either a Kaua‘i or O‘ahu origin for the *S. globosa* clade (Figure 17.26). The terminal three clades each had their origin on Kaua‘i, but rather than showing radiations on a single island, each clade dispersed to the younger islands of O‘ahu and the Maui Nui complex with some indication of a vicariant pattern within the complex. The only species occurring on the island of Hawai‘i is widespread and is found on Moloka‘i and Maui as well. The area cladogram fits the terminal resolution pattern, with an overall pattern of a radiation on Kaua‘i followed by dispersal first to O‘ahu and then to the islands of the Maui Nui complex. This apparent radiation on Kaua‘i may be the result of dispersal from an older island. If the cladograms produced in this analysis represent the actual phylogeny, repeated independent colonizations took place from an older island to the younger island of Kaua‘i. Therefore, if we eliminate the Kaua‘i taxa, the hypothetical location of the ancestor should shift to O‘ahu. When we remove the Kaua‘i taxa from the area cladogram, it shows that the lineage has four clades, each with an origin on O‘ahu (Figure 17.27). The two terminal clades (see Figure 17.26) each have widespread species as terminal taxa, and these are the only widespread species in the genus. Perhaps this is an example of the way such lineages evolve—terminal taxa dispersing to younger islands followed by allopatric speciation and radiation.

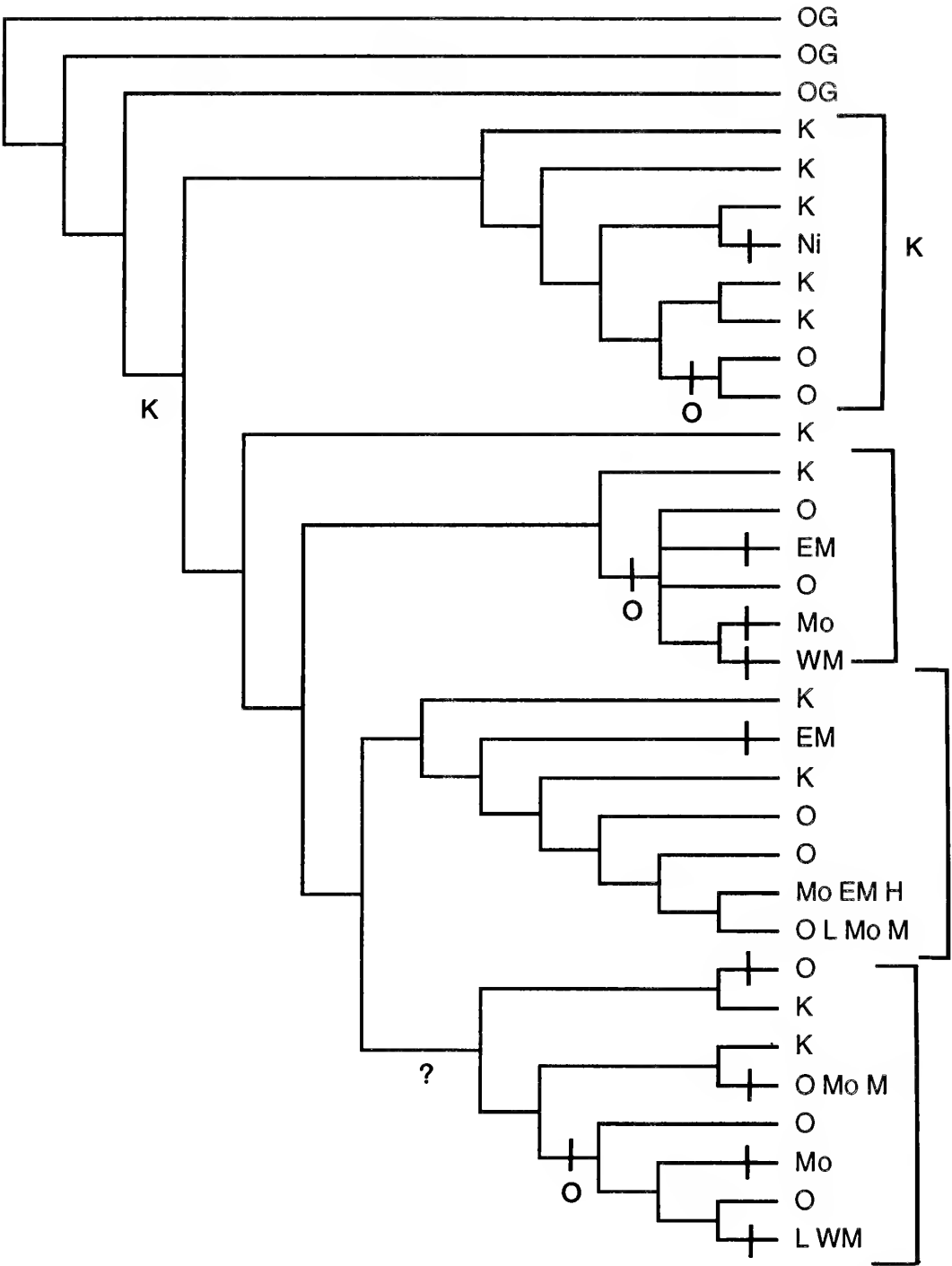


FIGURE 17.26. Area cladogram for *Schiedea* and *Alsinidendron*, data from Wagner et al. (Chapter 12). OG, outgroup; K, Kaua'i; Ni, Nihoa; O, O'ahu; Mo, Moloka'i; L, Lana'i, WM, West Maui; M, Maui; EM, East Maui; H, Hawai'i; the *question mark* indicates there is more than one equally parsimonious way to distribute the islands at that point on the area cladogram.

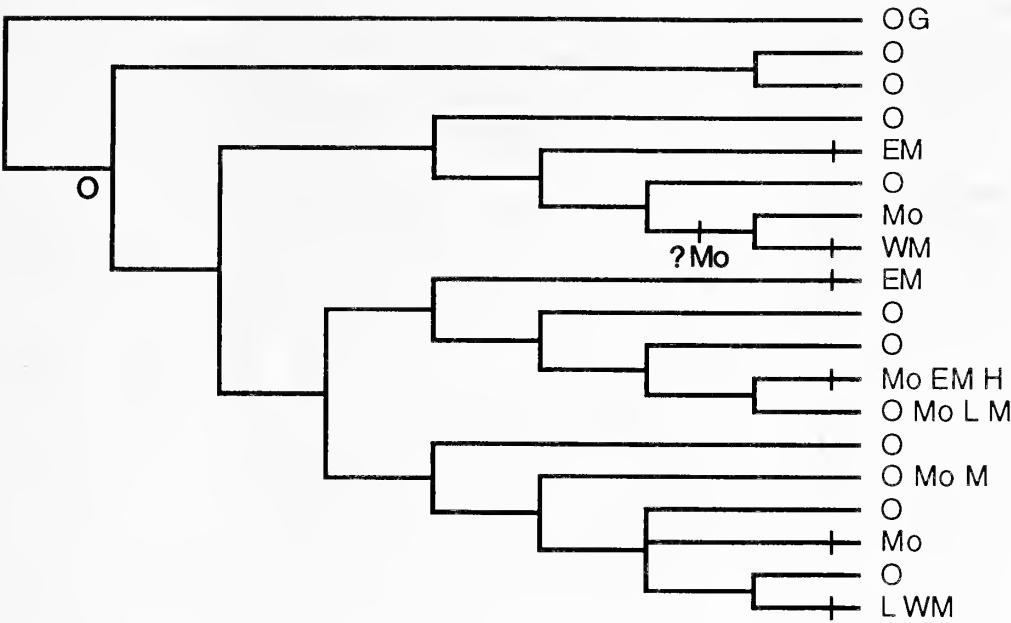


FIGURE 17.27. Area cladogram from Figure 17.26 after the removal of all the taxa found exclusively on Kaua'i. OG, outgroup; O, O'ahu; Mo, Moloka'i; L, Lana'i; WM, West Maui; M, Maui; EM, East Maui; H, Hawai'i; the *question mark* indicates there is more than one equally parsimonious way to distribute the islands at that point on the area cladogram.

Cyanea (Givnish et al., Chapter 14)

The area cladogram for *Cyanea* is one of the most-parsimonious cladograms (Figure 17.28). All the competing cladograms resolve the two main clades found in this diagram. The differences among these trees involve whether various groups of taxa are grades or clades. The area cladogram presented is one of the least resolved of any of the most-parsimonious trees. A biogeographic analysis of any of the other trees is consistent with results from the tree analyzed here.

In Figure 17.28, the clade with the fewest terminal taxa (clade A) has a Kaua'i grade at the base with two radiations, one on Kaua'i and the other on the islands of the Maui Nui complex. The second, larger clade (clade B) has a base on Kaua'i and an unresolved polytomy with three branches, one of which branches again, for a total of four clades. All four clades appear to represent radiations, one each on Kaua'i and O'ahu and two within the Maui Nui complex. The inter-island colonization pattern is difficult to determine because of the polytomy and because there are at least two, if not three, separate radiations within the Maui Nui complex involving both main clades. However, the two well-defined clades combined with the ambiguity of the relationships among the clades fits the

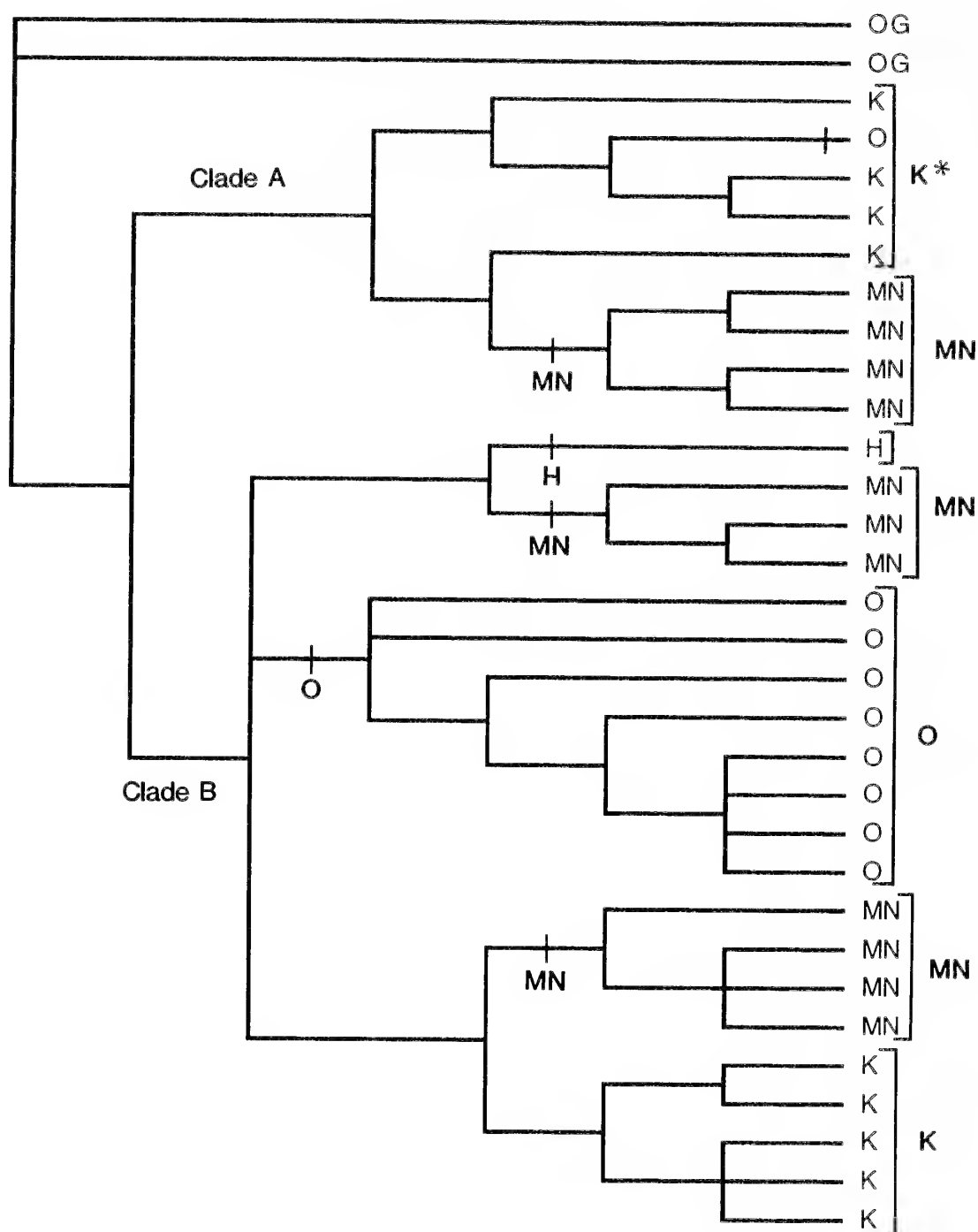


FIGURE 17.28. One of the equally parsimonious area cladograms for *Cyanea*, data from Givnish et al. (Chapter 14), with the two principal clades indicated as A and B. OG, outgroup; K, Kaua'i; O, O'ahu; MN, Maui Nui complex; H, Hawai'i; an *asterisk* denotes a group of taxa that form a grade, and all other groups are clades.

terminal resolution pattern and supports either an initial radiation on Kaua'i or an origin on an older island.

Sarona (Asquith, Chapter 7)

The area cladogram for *Sarona* (Figure 17.29) has a basal polytomy of five clades, each of which represents a radiation. This represents a termi-

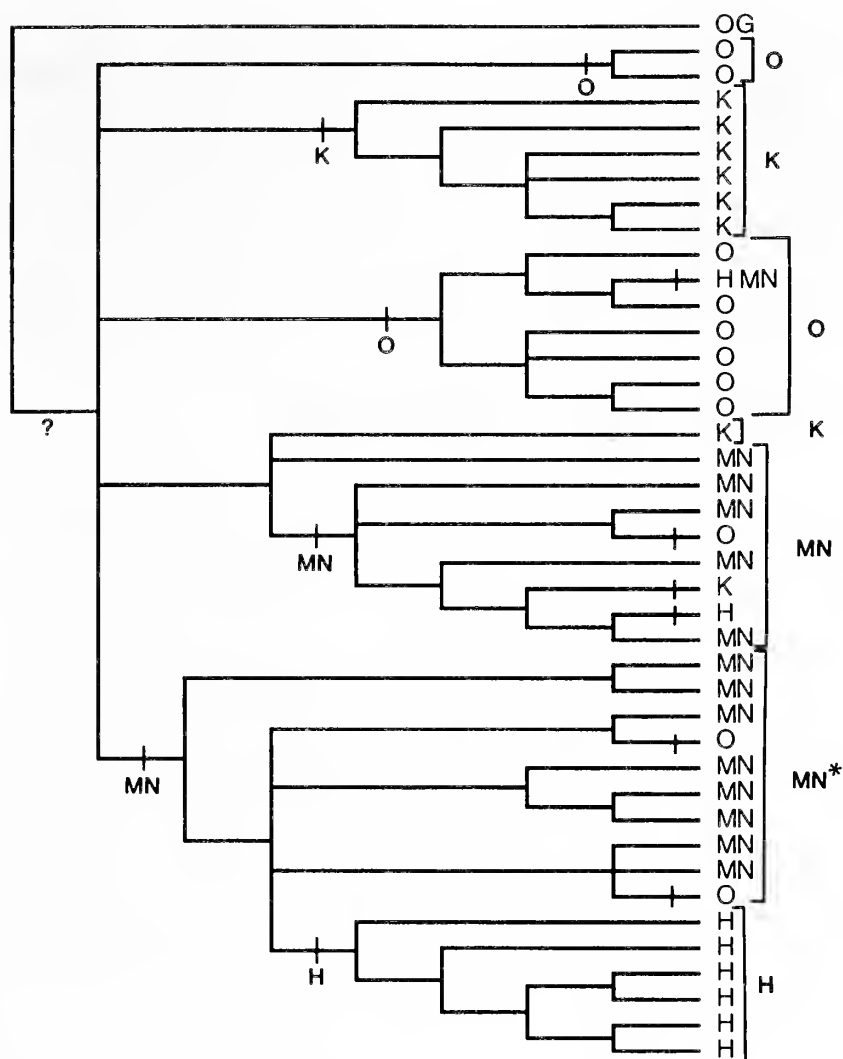


FIGURE 17.29. Area cladogram for *Sarona*, data from Asquith (Chapter 7). OG, outgroup; K, Kaua'i; O, O'ahu; MN, Maui Nui complex; H, Hawai'i; the *question mark* indicates there is more than one equally parsimonious way to distribute the islands at that point on the area cladogram; an *asterisk* denotes a group of taxa that form a grade, and all other groups are clades.

nal resolution pattern. The unresolved base may indicate early widespread dispersal of the ancestor or dispersal from an older, now-eroded island.

There are several distinctive features of the *Sarona* area cladogram. One of the groups in the basal polytomy shows a radiation on Kaua'i. Moreover, although the unresolved nature of the base makes several scenarios possible, none of the possibilities include an origin on the youngest island, Hawai'i. In fact, the only species on Hawai'i are in one of the clades of the terminal polytomy; this Hawai'i clade exhibits a radiation pattern. Radiations are also on O'ahu (with dispersal to the Maui Nui complex and Hawai'i) and within the Maui Nui complex. A back-dispersal occurs within the group to O'ahu. The central part of the

range by dispersal of the new species to different islands. As mentioned above, the same results are found using Kaua'i as the location of the ancestor of this clade, and only one additional inter-island dispersal event is required for either O'ahu or Hawai'i to be the location of the ancestor. Most likely, the ancestor of the core *Scaevola* clade colonized one of the main Hawaiian Islands, radiated on that island, and subsequently dispersed to most of the islands. It is possible that random dispersal would produce the stochastic pattern and that the species then dispersed to other islands; however, this is a less-parsimonious scenario.

Clermontia (Lammers, Chapter 15)

Most of the equally parsimonious area cladograms for *Clermontia* suggest a Hawai'i base, but a few of them were equivocal, with a Maui or Hawai'i origin. Thus, the resolution of all area cladograms clearly indicated an origin on a younger island. The cladogram (Figure 17.31) is poorly resolved, with very little information on the relationships among the taxa. This could be the result of either repeated dispersal from an older island or a widespread ancestor. Unlike other lineages investigated that had poorly resolved bases, this tree does not have either progressions or radiations in its terminal clades, so it does not fit the terminal resolution pattern. This clade is at least the result of a radiation on Hawai'i, with repeated back-dispersal to older islands.

Clermontia, however, is the sister group of the *Cyanea* clade (see Givnish et al., this volume, Chapter 14), and as such, they share a common ancestor. If *Cyanea* originated on Kaua'i or an even older island as the data seem to indicate, then either the ancestor of both genera was on the younger islands and back-dispersed to Kaua'i to give rise to *Cyanea* or the ancestor colonized Kaua'i or a pre-Kaua'i island. The ancestor of the extant species of *Clermontia* then dispersed to younger islands to give rise to the current species. If this is true, why are the current *Clermontia* species on older islands clearly derived via back-dispersal? The forest habitats where *Clermontia* species occur on younger islands appear very similar to forests on Kaua'i, suggesting that habitat availability is not the limiting factor. However, closer examination of older island forests suggests that there are ecological differences among the forests of ever-increasing ages (Mueller-Dombois, 1987). These ecological differences could make forests of older islands such as O'ahu and Kaua'i less suitable for successful colonization by or persistence of *Clermontia*. With the present area cladogram, it is difficult to speculate beyond the sup-

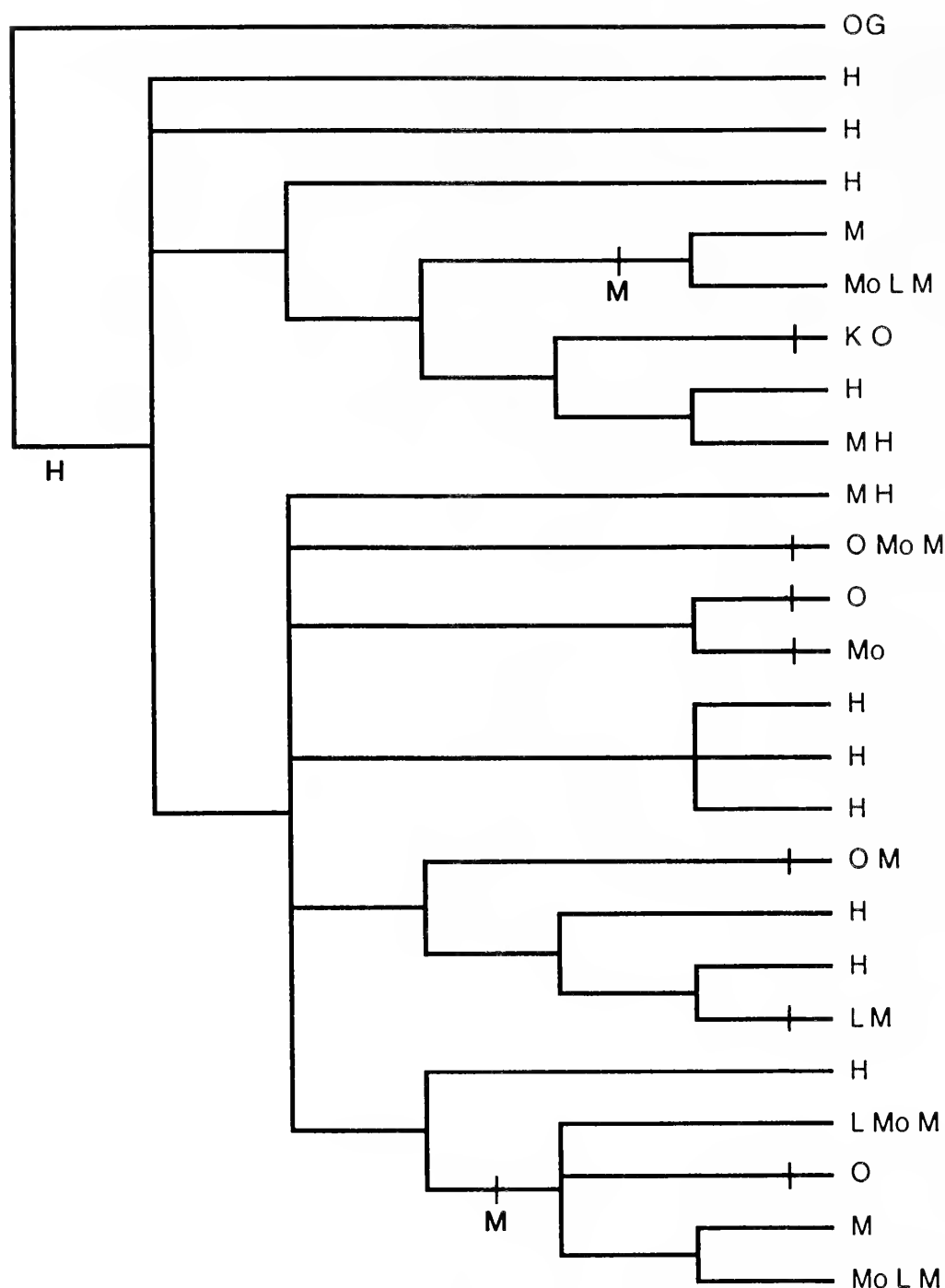


FIGURE 17.31. One of the equally parsimonious area cladograms for *Clermontia*, data from Lammers (Chapter 15). OG, outgroup; K, Kaua'i; O, O'ahu; Mo, Moloka'i; L, Lana'i; M, Maui; H, Hawai'i.

ported conclusion for the extant taxa—radiation on a younger island followed by back-dispersal.

Hawaiian *Tetramolopium* (Lowrey, Chapter 11)

There are 10 equally parsimonious cladograms for Hawaiian *Tetramolopium*. Two of the area cladograms are shown in Figure 17.32. All the area cladograms fall into one or the other of these two biogeographic patterns. Both cladograms show a younger island pattern with multiple

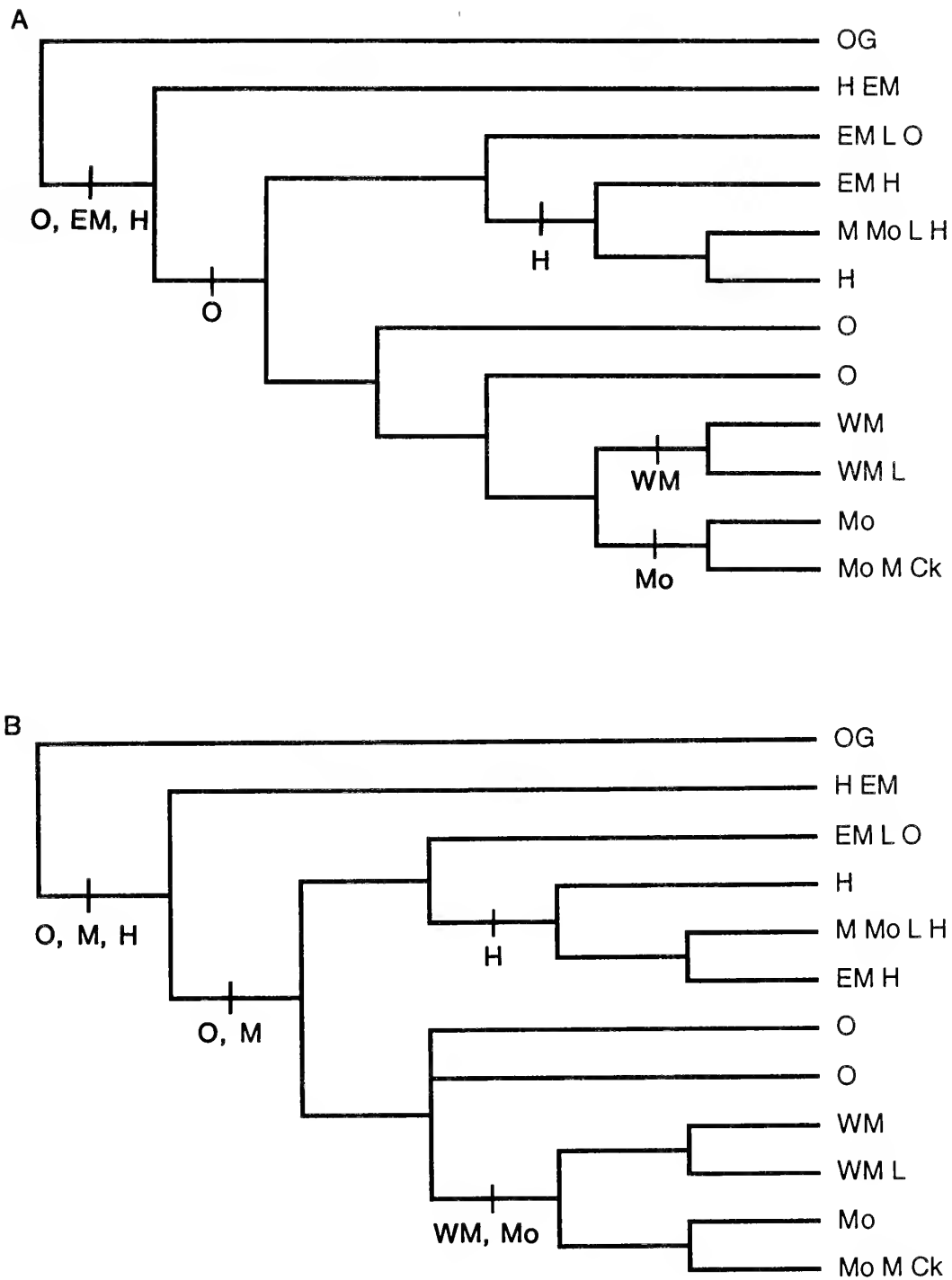


FIGURE 17.32. Two of the 10 equally parsimonious area cladograms for the Hawaiian species of *Tetramolopium*, data from Lowrey (Chapter 11). All area cladograms gave one or the other of these alternative results. (A) Area cladogram with an O'ahu ancestor for the two main subclades; (B) area cladogram with an equivocal ancestor for the two main subclades. OG, outgroup; O, O'ahu; Mo, Moloka'i; L, Lana'i; EM, East Maui; WM, West Maui; M, Maui; H, Hawai'i; Ck, Cook Islands.

dispersal events to older islands. Figure 17.32A shows an equivocal origin with inter-island dispersal associated with speciation to form a O,M,H \rightarrow O \rightarrow WM and Mo pattern and a separate pattern of O \rightarrow H. The second hypothesis (Figure 17.32B) is equivocal at most nodes including the base and differs largely from the first because of the different topology with an unresolved trichotomy in the lower subclade. Neither tree shows any semblance of a younger-to-older island pattern, which may be attributed to the dispersal ability of the taxa. Thus, this may be an example of the stochastic pattern. Other species of the genus are found on New Guinea and in the Cook Islands. The fact that the Hawaiian species form a monophyletic group (with one Hawaiian species also on the Cook Islands) and the close similarity of the *Tetramolopium* species suggest that the Hawaiian clade may represent a recent colonization pattern.

Both *Clermontia* and *Tetramolopium* exhibit similar biogeographic patterns in that both occur primarily on younger islands. Another shared feature is that in each clade, many species have multi-island distributions. There also is poor resolution of the island of origin of each clade. Finally, the patterns within these lineages are neither radiations nor progressions. Yet *Clermontia* possibly had an origin on an older island with only the current extant species on younger islands, whereas *Tetramolopium* appears to represent a recent colonization to the archipelago.

Platydesma (Funk and Wagner, Chapter 10)

Platydesma has two well-defined clades, but each has only two species; thus, biogeographic pathways are obscure (Figure 17.33). The area clado-

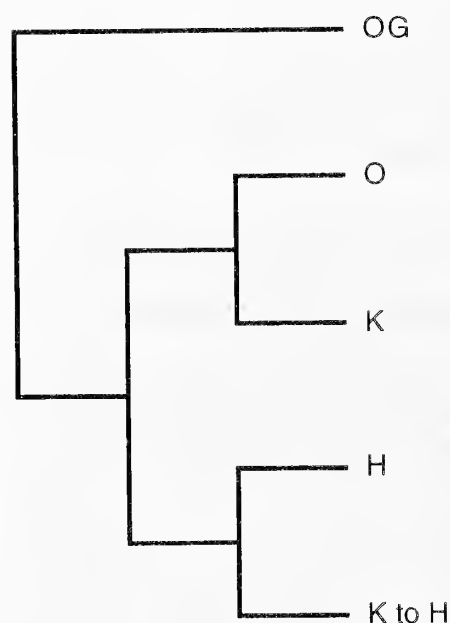


FIGURE 17.33. Area cladogram for *Platydesma*, data from Funk and Wagner (Chapter 10). OG, outgroup; K, Kaua'i; O, O'ahu; H, Hawai'i.

gram is compatible with several explanations; the one that seems best supported by morphology, however, is a Kaua'i, O'ahu, or perhaps a pre-Kaua'i radiation, followed by two independent dispersal events to younger islands of the archipelago.

SUMMARY OF PATTERNS

The following listing and Table 17.2 summarize the hypothetical patterns that were supported by the area cladograms.

Progression Rule Pattern

The basic progression rule pattern was found in the six lineages of *Drosophila* (also including a single radiation on Maui and two on Hawai'i), *Hesperomannia*, *Kokia* (with one back-dispersal), *Remya*, and the *spiny leg* clade of *Tetragnatha*.

Radiation Pattern

Five lineages exhibited a simple pattern of radiation: *Geranium*, honeycreepers (doubtfully), silverswords (*Argyroxiphium* and *Wilkesia*), *Platydesma*, and *Scaevola* (possibly). A number of other taxa exhibited a radiation as a secondary pattern (Table 17.2).

Unresolved Pattern

Only the genera *Clermontia* and *Sarona* presented cases that were basally unresolved. If *Clermontia* originated on Hawai'i, this group also exhibits one of the highest levels of back-dispersal.

Stochastic Pattern

Both *Tetramolopium* and the honeycreepers exhibited a stochastic pattern, but the basis differs. *Tetramolopium* apparently represents a recent colonization, whereas inter-island distances are not a significant dispersal barrier for the honeycreepers. It is less clear whether *Scaevola* fits this pattern or a radiation pattern. The current species of *Clermontia* exhibit a recent colonization pattern.

TABLE 17.2. Summary of Patterns Exhibited by Hawaiian Lineages Examined in This Book

| Base or single patterns | | |
|--|---|---|
| Progression rule | Radiation (cont.) | Back-dispersal |
| <i>Drosophila</i> | <i>Platydesma</i> | <i>Clermontia</i> |
| <i>Hesperomannia</i> | <i>Sarona</i> * | <i>Geranium</i> |
| <i>Hibiscadelphus</i> | <i>Scaevola</i> (possibly) | <i>Kokia</i> |
| <i>Kokia</i> | <i>Schiedea membranacea</i> | <i>Laupala</i> |
| <i>Remya</i> | clade* (doubtfully) | <i>Prognathogryllus</i> |
| <i>Tetragnatha</i> (2 spiny leg clades) | Silverswords | <i>Sarona</i> |
| Radiation | (<i>Argyroxiphium</i> and <i>Wilkesia</i>)* | <i>Scaevola</i> |
| <i>Clermontia</i> * | <i>Tetragnatha</i> * (elongate clade) | (possibly) |
| <i>Cyanea</i> * | | <i>Schiedea</i> |
| <i>Geranium</i> | Stochastic | <i>Tetragnatha</i> |
| <i>Hibiscadelphus</i> * | • High vagility | <i>Tetramolopium</i> |
| Honeycreepers | Honeycreepers (probably) | (possibly) |
| (doubtfully) | <i>Scaevola</i> (probably) | Unresolved |
| <i>Laupala</i> * | • Recent colonization | <i>Clermontia</i> |
| <i>Prognathogryllus</i> * (Maui and Hawai'i) | <i>Clermontia</i> | <i>Sarona</i> |
| | <i>Tetramolopium</i> | |
| Combined or special patterns | | |
| Progressive clades and grades | Terminal resolution (cont.) | Possible vicariant |
| <i>Drosophila</i> | <i>Sarona</i> | <i>Sarona</i> (Maui Nui complex) |
| <i>Laupala</i> | <i>Schiedea-Alsinidendron</i> | <i>Schiedea</i> (Maui Nui complex) |
| <i>Prognathogryllus</i> | Extinction | <i>Tetragnatha</i> (elongate clade, Maui Nui complex) |
| Silverswords (<i>Dubautia</i>) | <i>Clermontia</i> | |
| <i>Tetragnatha</i> | <i>Geranium</i> (possibly) | |
| Terminal resolution | <i>Schiedea membranacea</i> | |
| <i>Cyanea</i> | clade (possibly) | |
| <i>Drosophila</i> (overall) | Silverswords | |
| | (<i>Argyroxiphium</i>) | |

Notes: Asterisks indicate secondary patterns within terminal clades in an overall lineage. Parenthetical notations indicate the extent or portion of the lineage involved, or in some cases, the level of uncertainty about the pattern detected (e.g., if it is thought to be an artifact of weak data or other compounding factors).

Back-Dispersal Pattern

Many of the lineages have one or a few species that appear to be the result of back-dispersal, including *Clermontia*, *Geranium*, *Kokia*, *Laupala*, *Prognathogryllus*, *Sarona*, *Schiedea*, *Tetragnatha*, and possibly *Tetramolopium* and *Scaevola*. Although there are a few documented back-dispersal

events in these cladograms, they are usually to the next older island. The greatest distance back-dispersal event among the main islands would be from Hawai'i to Kaua'i. Examining all the lineages, we find that there is only one event that is unequivocally a back-dispersal from Hawai'i to Kaua'i: *Prognathogryllus*, in which a single Kaua'i species is embedded in a clade of Hawai'i species. A second, less clear case is *Kokia*. The other potential examples have sister species separated by less overall dispersal distance.

Progressive Clades and Grades Patterns

Progressive clades and grades are treated together because both result from radiations and differ only in which taxon of the group is involved in dispersal to another island. Several of the taxa fit this pattern, including the *elongate* clade of *Tetragnatha* (which also exhibits radiations on the Maui Nui complex and Hawai'i), both *spiny leg* clades of *Tetragnatha* (one of which includes a radiation on East Maui, the other a radiation on Maui), *Prognathogryllus* (including radiations on Kaua'i, O'ahu, Maui, and Hawai'i), *Laupala* (including radiations on Kaua'i, O'ahu, Maui, and Hawai'i), *Hibiscadelphus* (including a radiation on Hawai'i), and *Dubautia* (including radiations on Kaua'i, the Maui Nui complex, and Hawai'i).

Terminal Resolution

Taxa showing a terminal resolution pattern have several well-defined clades, but there is no clear inter-island progression rule evident as an overall pattern. Instead, the overall pattern is either a radiation or unresolved. Included in this category are the *Schiedea-Alsinidendron* clade, *Sarona*, *Cyanea*, and probably the Drosophilidae. In *Schiedea* and *Alsinidendron*, the basal pattern is one of a radiation on Kaua'i with a basal clade and grade on Kaua'i and three clades that each follow the progression rule. *Sarona* has a basal pattern that is unresolved, and clades are radiations, including two on Kaua'i, one on O'ahu, and three on the Maui Nui complex. An intermediate example is *Cyanea*, which has a well-resolved basal dichotomy that gives the area cladogram a Kaua'i base but otherwise has a mostly unresolved pattern within the largest clade (clade B, Figure 17.28). Although unresolved, clade B has four clades that are radiations, two on Maui Nui, one on O'ahu, and one on Kaua'i. Clade A has a grade on Kaua'i and a clade on the Maui Nui complex. Perhaps the pattern in *Cyanea* best illustrates why the two basal

patterns are treated together. The difference depends on how closely related the original ancestors of the clades were and whether they retained any of their unique characters.

One group that will eventually fall into the terminal resolution category is the overall pattern for DeSalle's six clades of *Drosophila*. Each clade has a progression rule pattern, but at this time, the overall pattern has not been analyzed well enough to determine whether the basal pattern will be a radiation or unresolved.

Recent Colonization

Tetramolopium appears to be the only lineage examined in this volume that clearly exhibits a pattern of recent colonization to the archipelago, although if *Geranium* has not experienced older-island extinctions, it too would exhibit a recent colonization pattern.

Extinction

The absence of sources of information such as a fossil record hamper a valid assessment of extinction. However, the analyses suggest an extinction pattern for several groups including *Clermontia*, *Geranium*, *Argyroxiphium*, and apparently, the *Schiedea membranacea* lineage.

HIGHER-LEVEL SIMILARITY IN BIOGEOGRAPHIC PATTERNS

Study of all the patterns suggests that several overall groupings of the area cladograms can be made. First, how well supported are the two most common patterns, progression and radiation? There are four examples of radiation as a basic pattern. The honeycreepers may have a radiation on Kaua'i, an old island. *Geranium* and *Argyroxiphium* have radiations on East Maui, a young volcano (but both clades may have had their origin on an older island). *Scaevola* has a single-island radiation pattern, but the species have dispersed to other islands, making determination of the island where the original radiation took place impossible.

Radiation (intra-island speciation) in general has played an important role in the diversification of the Hawaiian biota. For instance, several groups had major radiations on multiple islands. The largest of these were found in *Sarona*, *Cyanea*, the two cricket genera *Prognathogryllus* and *Laupala*, the *elongate* clade of *Tetragnatha*, and the *Dubautia-Wilkesia* clade of the silversword alliance. *Sarona* and *Cyanea* had a

largely ambiguous overall inter-island pattern, and the other taxa followed the progression rule. If one totals the number of radiations across all groups studied that have 3 or more species on a single island, including the single-island radiation clades, then Kaua'i has 6, O'ahu has 4 or 5, Maui has 7 (and the rest of the Maui Nui complex has an additional 6, for a total of 13 for the entire Maui Nui complex), and Hawai'i has 6. In most groups, the Hawai'i radiations were one of the terminal branches of the cladogram. O'ahu shows the fewest number of radiations, either four or five (one in each of the cricket genera, one in *Sarona*, one in *Cyanea*, and perhaps one in *Schiedea*). There is no clear reason why this should be so, except that O'ahu has experienced a much greater habitat alteration beginning with the arrival of the Polynesians and continuing to the present, which may have caused differential extinctions.

The progression rule was also common. Eighteen of the 25 lineages studied have an area cladogram that follows the progression rule either as an overall pattern or as a subpattern. Four of the 25 lineages have a single-island radiation pattern, so are excluded from this count. Among the remaining three lineages, *Tetramolopium* is probably a recent introduction to the archipelago, *Clermontia* may represent an extinction pattern (but one difficult to distinguish from that of a recent colonization pattern), and *Platydesma* breaks into two two-taxa statements (so is agreeable to many patterns, including the progression rule).

What is the balance between inter-island dispersal events associated with speciation and intra-island radiation? In the data sets included in this volume, slightly more than 100 events of inter-island dispersal are associated with speciation and there are slightly more than 200 intra-island events, for an approximate ratio of 1:2.

How important are habitat shifts and inter-island dispersal in promoting speciation? In the case of inter-island dispersal, isolation may be great enough to allow speciation without habitat shifts. If so, a greater number of habitat shifts should be observed in intra-island radiations than in inter-island diversification. Hawaiian *Drosophilidae* represent one end of the spectrum in that most speciation has occurred with colonization of a new island. This has suggested the idea of genetic destabilization accompanying a founder dispersal to new islands, which may be sufficient to promote speciation (Carson, 1987a). Several authors have contrasted intra- and inter-island speciation with habitat shifts. At least several of the plant groups, including *Cyanea*, *Geranium*, *Schiedea*, and the silversword alliance, have documented habitat shifts associated with speciation, and shifts appear to be more frequent with intra-island

radiations. Similar ecological shifts have been documented in many of the other taxonomic groups studied here, and at least some of them show a greater tendency for shifts to occur in intra-island radiations. *Sarona*, the *elongate* clade of *Tetragnatha*, and the cricket genera provide examples in that host plant shifts or ecological or behavioral shifts appear to occur more commonly in intra-island radiations. How common this is in other groups that have radiations on single islands is not certain but surely warrants investigation.

Several findings should be viewed with caution by evolutionary biologists who work on interspecific relationships without a phylogeny. Even in such closely related groups as the members of a lineage on the Hawaiian Islands, one cannot be sure that species from the same lineage on the same island are closely related to one another. They could be sister taxa, but they could also be members of different radiations (e.g., *Cyanea*), individuals from different progressions (e.g., *Schiedea*), the result of back-dispersal (e.g., *Sarona*), or even independent dispersals from another island (e.g., honeycreepers).

CONCLUSIONS

The most frequent pattern found among the lineages presented in this volume is one of dispersal from older to younger islands in the form of the progression rule and progressive clades and grades. There are also several potential older island patterns and several instances of back-dispersal and single-island radiation patterns. Many lineages exhibited radiations on individual islands that can be investigated for adaptive radiation and vicariance.

Clearly, the investigations in this volume have demonstrated very strong patterns in biological diversification on this hot spot archipelago, many of which are consistent with one another. The most common patterns are progression, radiation, and combinations of the two. Judging from the species-rich groups examined in this volume, speciation on the Hawaiian Islands occurs approximately one-third inter-island and two-thirds intra-island.

Finally, evidence indicates that the geologic history of the islands has a very powerful influence on the evolutionary history of successful colonists. More important, these studies have shown that one can tell when the influence of geology is important to radiation and when it is not. The results of these analyses show that phylogenetic analysis can be very informative concerning the relationship between the phylogeny of

the Hawaiian organisms and the geologic history of the islands. Furthermore, they show the use of phylogenetic systematics as a method for examining the evolutionary history of organisms.

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Postscript

The Hawaiian Islands, like most of the Pacific, have experienced major perturbations of the biota, resulting in tragic loss of species and ecological stability (Cuddihy and Stone, 1990; Wagner, 1991). The lowland, especially leeward, areas of islands have suffered the greatest losses. Today, cattle pastures occupy approximately 50% of the land area of the Hawaiian Islands, plantations and urban areas account for about another 30%, and the remaining 20% harbor native and introduced plant communities (Gagné and Cuddihy, 1990). The sheer magnitude of the changes can be appreciated in that approximately half the species of flowering plants that grow outside of cultivation in the Hawaiian Islands are alien (Wagner et al., 1990) and roughly 40% of the insect fauna consists of introduced species (Howarth and Mull, 1992). The situation in more mesic upland habitats is somewhat better than in the lowlands, but all the biota has been greatly affected. As a result, our study of the Hawaiian biota will have information gaps and bias.

The problem relative to the analyses here is that we do not know the extent of the changes in species diversity fostered by the early Polynesians before collection and scientific study of the biota. There is no doubt that the early Hawaiians greatly altered the lowland vegetation of the Hawaiian Islands, particularly during the period of greatest growth in population and expansion of agriculture between 1100 and 1650 A.D. (Kirch, 1982, 1983, 1985; Cuddihy and Stone, 1990). The destruction of native ecosystems has accelerated during the past 200 years in the Hawaiian Islands since the arrival of James Cook, largely through continued habitat alteration and the effects of feral mammals, insects, and plants.

The fauna, at least in the Hawaiian Islands, has not fared well. One of the best-known studies of the tremendous changes brought about after humans arrived in the archipelago is the study of fossil birds. Olson and James (1982a,b) found 40 previously unknown extinct species of birds from primarily lowland sites. Radiocarbon dating of the fossils indicates that many of these species became extinct after the Polynesian coloniza-

tion of the islands. This means that more than half the endemic land birds that were present before the arrival of the Polynesians became extinct before the arrival of the Europeans (Olson and James, 1982a,b, 1991; James and Olson, 1991). On O'ahu, land snail fossil deposits indicate similarly extensive changes in the snail fauna during the Polynesian period, with some species decreasing and others, adapted to disturbance, increasing (Kirch, 1983). Approximately half the 1,000 species of endemic Hawaiian land snails appear to be extinct (Gagné and Christensen, 1985). Less is known about the fate of the Hawaiian arthropod fauna. Estimates of extinction are particularly difficult in arthropods because large numbers of taxonomic groups have not been well studied. It is clear, however, that native arthropod communities have been greatly affected but do not appear to be as susceptible to extinction as the land snails or birds. The reasons that snails are so susceptible to extinction are low fecundity, low vagility, and especially habitat destruction. Birds are also affected by habitat loss and alteration, but disease appears to be another significant factor.

There is no comparable body of fossil studies on the flora like the bird work, so we can only guess the degree of its extinction during human occupation of the Hawaiian archipelago. Among the few Hawaiian paleobotanical studies are the pollen corings made by Selling (1948), although others are currently under way by several researchers, including S. Athens, R. Byrne, and J. Ward.

Although we cannot yet reliably estimate the extent to which the alterations on these oceanic islands have caused extinctions, it is clear that distributions were drastically altered. Such disturbances affect biogeographic analysis by altering the distributions of the taxa under investigation. However, they do not alter the relationships among the taxa investigated, nor do they negate the information from the biogeographic interpretations. The knowledge of these extinctions provides a warning that the conclusions from these studies should always be considered in the light of the possibility of range reductions and species extinctions. Despite the problems, studies such as those presented in this volume are worthwhile not only for their intrinsic scientific value but also for insights in the continued efforts to conserve what remains of this fascinating biota.

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